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- FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)



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CRETACEOUS FAUNAS FROM ZULULAND  
AND NATAL, SOUTH AFRICA  
THE AMMONITE SUBFAMILY TEXANITINAE  
COLLIGNON, 1948

By

HERBERT CHRISTIAN KLINGER

&

WILLIAM JAMES KENNEDY

Cape Town Kaapstad



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SOUTH AFRICA

THE AMMONITE SUBFAMILY TEXANITINAE COLLIGNON, 1948

By

HERBERT CHRISTIAN KLINGER

*South African Museum, Cape Town*

&

WILLIAM JAMES KENNEDY

*Geological Collections, University Museum, Oxford*

(With 269 figures)

[MS. accepted 14 September 1979]

ABSTRACT

Ammonites referred to the subfamily Texanitinae Collignon, 1948, are the dominant macrofaunal element in rocks of Upper Coniacian to Middle Campanian age in Zululand, Natal, and Pondoland, and are of extreme interest as far as intraspecific variation, evolutionary trends, apparent endemism and gigantism are concerned. The subfamily is represented by thirty-seven species belonging to the following genera and subgenera: *Protexanites* s.s., *Paratexanites*, *Plesiotechanites*, *Reginaites*, *Texanites*, *Submortonicer*, *Bevahites*, *Menabites* s.s., *M. (Australiella)* and *M. (Delawarella)*. Subtle differences exist between the Pondoland and Zululand specimens, and these are here separated at subspecific level. Thirteen new species and three new subspecies are described; these are—new species: *Paratexanites australis*, *P. pseudotricarinatum*, *Plesiotechanites collignoniforme*, *P. matsumotoi*, *Reginaites reymonti*, *R. zulu*, *Texanites collignoni*, *T. vanhoepeni*, *T. postvanhoepeni*, *T. umzambiense*, *Bevahites? enigma*, *Menabites (Delawarella) gigas*, *M. (Delawarella) nibelae*; new subspecies: *Texanites presoutoni presoutoni*, *T. presoutoni natalense*, *T. soutoni natalense*; and *Reginaites? sp. nov.*? cf. *Plesiotechanites stangeri* (Baily).

Evolutionary trends are discussed within the Texanitinae as shown by the South African faunas. The geographic distribution of the subfamily shows it to be highly endemic and prolific towards the end of the Santonian and during the Lower and Middle Campanian, shortly before its demise.

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INTRODUCTION

Ammonites referred to the subfamily Texanitinae Collignon, 1948, are the dominant macrofaunal element in the Upper Coniacian to Middle Campanian sediments of southern Africa, both in terms of numbers of individuals



and species, and are of extreme interest as far as intraspecific variation, evolutionary trends, apparent endemism and gigantic growth are concerned. Furthermore, identification of these faunas allows for detailed stratigraphic correlation with biostratigraphically equivalent strata of Madagascar, and to a very limited extent those of western Europe, the Gulf Coast regions of North America, and Hokkaido, Japan.

The authors were struck by the bewildering array of intraspecific variation in the texanitine material at their disposal. Features such as density of ribbing and tuberculation, presence or absence of bifurcations or intercalations, and even relative proportions, which, by current ammonoid classification standards, would be of specific or even generic value, were found to be of relatively minor taxonomic significance if viewed in their proper stratigraphic context. This does not imply that the authors negate the possibility of more than one species being found at the same stratigraphic level, but rather emphasizes that specific identity should be viewed in terms of consanguinity of characters rather than typologically. In this respect, the authors were hampered somewhat because a large proportion of the available material is from older collections, primarily that of the late Dr E. C. N. van Hoepen, which lack precise stratigraphic data. Detailed collecting by the authors during several field seasons alleviated this shortcoming to some degree.

In addition to the extreme intraspecific variation, a biogeographic separation into a northern Zululand fauna frequenting the deeper water facies of the St Lucia Formation of the False Bay region, and a southern fauna frequenting the shallower water of the transgressive Umzamba Formation of Pondoland, Transkei, becomes apparent.

In identifying the South African material, the authors made extensive use of the monographical studies of Collignon (1948), and the Santonian and Campanian parts of his subsequent series *Atlas des fossiles caractéristiques de Madagascar (Ammonites)* (1966a, 1969, 1970), Young's (1963) description of the Upper Cretaceous faunas of the Gulf Coast of America, and Matsumoto's (1970) recent description of the Texanitinae from Hokkaido.

Unfortunately, the majority of texanitine species seems to be endemic, thus precluding precise stratigraphic correlation on a global scale. Similarities between the South African and Malagasy material are striking, and Collignon's biostratigraphic zonation compiled for Madagascar could be employed to good effect. This notwithstanding, a great proportion of the material appears to be new, necessitating the erection of new species.

The association of the form genus *Spinaptychus* Trauth with representatives of the subfamily Texanitinae is firmly established on the basis of more material to supplement previous records by the authors (Klinger 1972, Kennedy & Klinger 1972).

Broad outlines of the evolution and evolutionary trends within the Texanitinae, as displayed by the South African material and aspects of the palaeobiogeography of the subfamily are discussed after the systematic descriptions.



### LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

|      |   |
|------|---|
| BMNH | British Museum (Natural History), London.   |
| NMB  | National Museum, Bloemfontein (presently housed in the collections of the South African Museum, Cape Town). |
| OLL  | Oberösterreichisches Landesmuseum, Linz.  |
| SAM  | South African Museum, Cape Town.  |
| SAS  | Geological Survey of South Africa, Pretoria.  |
| TM   | Transvaal Museum, Pretoria.   |
| UN   | Geology Department, University of Natal, Durban.  |

### FIELD LOCALITIES

Details of field localities referred to in the text are provided in Kennedy & Klinger (1975). Full descriptions of the localities are housed in the libraries or collections of the British Museum (Natural History), Geological Survey of South Africa (Pretoria), and the South African Museum.

### DIMENSIONS OF SPECIMENS

Dimensions of specimens are given in millimetres; abbreviations are as follows:

D = diameter, Wb = whorl breadth, Wh = whorl height, Wb:Wh = ratio of whorl breadth to whorl height, U = umbilical diameter.

Figures in parentheses are dimensions as a percentage of total diameter.

### SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916; see Kullmann & Wiedmann 1970 for a recent review) is followed in the present work:

I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

### ANNOTATION OF ORNAMENTATION

Terminology of tuberculation followed here is essentially the same as that of Collignon (1948: 55), and Young (1963: 37, text-fig. 6), reproduced here in slightly modified form as Figure 1. Tubercles are numbered sequentially from the umbilical wall ventrally towards the keel; the umbilical tubercle (Ut) is number 1, the lateral tubercle (Lt) 2, the submarginal (St) 3, the marginal (Mt) 4, and the external (Et) 5. This is a genetic annotation. In genera lacking the lateral tubercle, the second tubercle encountered ventrally from the umbilical wall is situated submarginally, and thus annotated as number 3. Similarly, in genera where two or more tubercles arise through division of a single tubercle, the latter is referred to according to its position, e.g. ventrolateral, with the

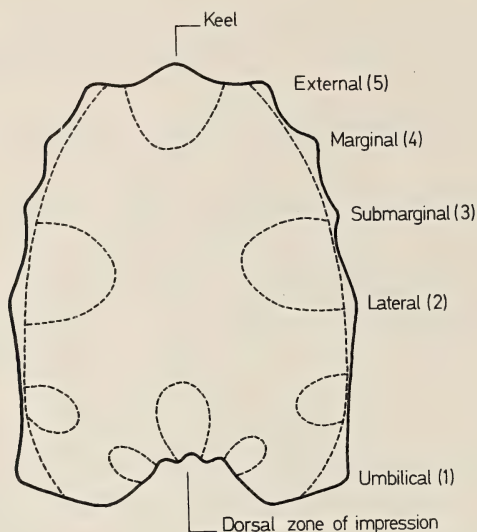


Fig. 1. Whorl section of a texanite ammonite to explain annotation regarding ornamentation used in the text; modified after Collignon (1948: 55) and Young (1963: 37, text-fig. 6).

numbers of the tubercles it eventually gives rise to in parentheses, e.g. (3+4), (2, 3, 4).

Rib-counts are indicated as the number of internal (Int.) (umbilical) tubercles versus the number of external (Ext.) tubercles. It was found impracticable to annotate and count ribbing in terms of bifurcating and/or intercalatory ribs as the distinction between these is often slight and generally of subordinate importance in texanite systematics.

## SYSTEMATIC PALAEONTOLOGY

### Phylum **MOLLUSCA**

#### Class **CEPHALOPODA**

#### Subclass **AMMONOIDEA** Zittel, 1884

#### Superfamily **ACANTHOCERATACEAE** de Grossouvre, 1894

#### Family **Collignoniceratidae** Wright & Wright, 1951

#### Subfamily **Texanitinae** Collignon, 1948

The subfamily Texanitinae is a prolific group, ranging in age from ?Lower Coniacian to Middle Campanian, and is best known from Madagascar, the Gulf Coast regions of North America, and Hokkaido, Japan. The subfamily is herein taken to include the following genera and subgenera:



*Texanites* Spath, 1932  
*Paratexanites* Collignon, 1948  
*Bevahites* Collignon, 1948  
*Submorticeras* Spath, 1921  
*Menabites* s.s. Collignon, 1948  
*Menabites* (*Bererella*) Collignon, 1948  
*Menabites* (*Delawareella*) Collignon, 1948  
*Menabites* (*Australiella*) Collignon, 1948  
*Protexanites* s.s. Matsumoto, 1955  
*Protexanites* (*Miotexanites*) Matsumoto, 1970  
*Protexanites* (*Anatexanites*) Matsumoto, 1970  
*Protexanites* (*Pleurotexanites*) Matsumoto, 1970  
*Plesiotexanites* Matsumoto, 1970  
*Reginaites* Reyment, 1958  
*Defordiceras* Young, 1963

Obvious synonyms of these taxa are discussed in the text. Initially, the subfamily Texanitinae formed a relatively homogeneous group, consisting of unicarinate trituberculate to pentatuberculate taxa, but lately through the inclusion of *Reginaites*, *P. (Pleurotexanites)*, and *Defordiceras*, the definition has to be modified to accommodate these tricarinate, interrupted unicarinate, and keel-less forms.

Generic subdivision is based mainly on the number of rows of tubercles.

*Protexanites* is trituberculate throughout, except in *P. (Anatexanites)* where a lateral (2) row of tubercles is added in later stages. *Paratexanites* is quadrituberculate throughout, lacking the lateral (2) row of tubercles. *Texanites* is pentatuberculate from an early stage, as is *Submorticeras*, but in the latter, lateral ornament weakens in later stages of growth. *Plesiotexanites* links between *Paratexanites* and *Texanites* in forming a lateral tubercle after variable stages of growth. *Bevahites* and *Menabites* s.l. differ from the other genera in having more tubercles in the external (5) row than in the other rows. In *Bevahites* the marginal (3) and submarginal (4) tubercles remain more or less approximated throughout, thus differing from *Menabites*. *Reginaites* is bituberculate to quadrituberculate, as here interpreted, but is distinctly tricarinate as in *Peroniceras*. This latter similarity is an example of homoeomorphy and not genetic affinity. *Defordiceras* lacks a keel on the outer whorls. Whether this condition also prevails on the inner whorls is unknown.

The suture throughout is relatively simple with a primary suture formula  $ELU_2U_1I$ .

The following species are described from South Africa:

*Protexanites cyni* (van Hoepen)  
*Paratexanites australis* sp. nov.  
*Paratexanites pseudotricarinatum* sp. nov.  
*Paratexanites umkwelanense* (Crick)

- Paratexanites* sp. aff. *P. emscheris* (Schlüter)  
*Paratexanites* sp. aff. *P. serratomarginatus* (Redtenbacher)  
*Plesiotexanites stangeri* (Baily)  
*Plesiotexanites collignoniforme* sp. nov.  
*Plesiotexanites matsumotoi* sp. nov.  
*Plesiotexanites?* sp. indet.  
*Reginaites reymonti* sp. nov.  
*Reginaites zulu* sp. nov.  
*Reginaites?* sp. nov. ? cf. *Plesiotexanites stangeri* (Baily)  
*Texanites collignoni* sp. nov.  
*Texanites quadrangulatus* Collignon  
*Texanites vanhoepeni* sp. nov.  
*Texanites postvanhoepeni* sp. nov.  
*Texanites rarecostus* Collignon  
*Texanites texanus* (Roemer)  
*Texanites umzambiense* sp. nov.  
*Texanites presoutoni presoutoni* ssp. nov.  
*Texanites presoutoni natalense* ssp. nov.  
*Texanites soutoni soutoni* (Baily)  
*Texanites soutoni natalense* ssp. nov.  
*Submortonicerias woodsi* s.l. (Spath)  
*Submortonicerias condamyi* s.l. (Collignon)  
*Bevahites?* *enigma* sp. nov.  
*Bevahites* sp. A. gr. ex. *B. subquadratus* Collignon  
*Bevahites* sp. B. gr. ex. *B. subquadratus* Collignon  
*Menabites (Menabites) boulei* Collignon  
*Menabites* s.l. sp. juv. indet.  
*M. (Australiella) australis* (Besairie)  
*M. (Australiella) falloti* (Collignon)  
*M. (Delawarella) delawarensis* (Morton)  
*M. (Delawarella) subdelawarensis* Collignon  
*M. (Delawarella)* sp. aff. *M. (D.) jeanneti* Collignon  
*M. (Delawarella) gigas* sp. nov.  
*M. (Delawarella) nibelae* sp. nov.  
*M. (Delawarella)* sp. indet.

#### Genus *Protexanites* Matsumoto, 1955

##### *Type species*

*Ammonites bourgeoisi* d'Orbigny, 1850, by original designation of Matsumoto (1955: 38).

##### *Discussion*

The genus *Protexanites* was originally erected by Matsumoto (1955) for species 'similar to *Texanites* in general aspect . . . typically trituberculate . . .



and sometimes quadrituberculate in the later whorls with one lateral tubercles [sic] in addition to the other three' (Matsumoto 1955: 38). Since then, however, more material has become available and Matsumoto (1970: 227–228) now recognizes four distinct subgenera:

*Protexanites* s.s. Matsumoto, 1955 (type species *Ammonites bourgeoisi* d'Orbigny, 1850).

*Anatexanites* Matsumoto, 1970 (type species *Mortoniceras fukazawai* Yabe & Shimizu, 1925).

*Miotexanites* Matsumoto, 1970 (type species *Protexanites* (*Miotexanites*) *minimus* Matsumoto, 1970).

*Pleurotexanites* Matsumoto, 1970 (type species *Protexanites superbus* Collignon, 1966a).

Differences between the various subgenera are distinct. *Protexanites* s.s. is trituberculate throughout; *Anatexanites* acquires a lateral (2) tubercle at varying stages of growth; in *Miotexanites* the development of the ventrolateral tubercle is retarded, and in *Pleurotexanites* the tubercles of the external (5) row outnumber those of the umbilical (1) or submarginal (3) rows; in addition, the keel, consisting of a line of multiplied tubercles, is interrupted.

Only representatives of *Protexanites* s.s. occur in southern Africa, hence the reader is referred to Matsumoto (1970) for discussions on the limits and affinities of the other three subgenera. Species referred to these latter subgenera by Matsumoto (1970) are:

#### Subgenus *Anatexanites*

*P. (Anatexanites) fukazawai* (Yabe & Shimizu) (1925: 130, pl. 30 (fig. 1), pl. 31 (figs 1–2, 6–7, non 3), pl. 33 (figs 1–2)) from the Middle Santonian of Kyushu and Hokkaido.

*P. (Anatexanites) nomii* (Yabe & Shimizu) (1925: 131, pl. 32 (figs 1–3)) from the Santonian of Hokkaido.

*P. (Anatexanites) reymenti* Matsumoto, 1970 (= *Texanites* cf. *quattuornodosus* in Reyment 1955: 93, pl. 23 (fig. 3), text-fig. 46a) from the Santonian of southern Cameroons.

#### Subgenus *Miotexanites*

*Protexanites* (*Miotexanites*) *minimus* Matsumoto (1970: 246, pl. 33 (figs 1–3), text fig. 8) from the Coniacian or Lower Santonian of Hokkaido.

? *Niceforoceras* (?) *japonicum* Matsumoto (1965: 71, pl. 11 (fig. 1) text-fig. 40) from Hokkaido may be an example of *Miotexanites*.

#### Subgenus *Protexanites* Matsumoto, 1955

##### *Type species*

*Ammonites bourgeoisi* d'Orbigny, 1850, by the original designation of Matsumoto (1955: 38).

### Diagnosis

Following the very early smooth stages, ornament consists of single, bifurcating or intercalatory ribs bearing three rows of tubercles only; umbilical (1), submarginal (3), and external (5). The keel may be entire or crenulate. Primary suture quinquelobate with formula  $ELU_2U_1I$ .

### Discussion

Matsumoto (1970: 228) referred the following species to *Protexanites* s.s.: *P. (Protexanites) bontanti* (de Grossouvre) (1894: 77, pl. 17 (fig. 2 only)) from the Coniacian of France.

*P. (Protexanites) bourgeoisi* (d'Orbigny, 1850) (De Grossouvre 1894: 73, pl. 13 (fig. 2), pl. 14 (figs 2–5)) from the Senonian of France.

*P. (Protexanites) canaensis* (Gerhardt) (1897: 73, pl. 1 (fig. 2a–c)) from the Lower Senonian, presumably Coniacian, of Venezuela.

*P. (Protexanites) peroni* Matsumoto, 1970 (= *Peroniceras czoernigi* Peron non Redtenbacher, 1896: 53, pl. 11 (figs 7–8)) from the base of the Senonian of Djebel Aures, Algeria.

*P. (Protexanites) shoshonense* (Meek) (1876: 449, pl. 6 (figs 3a, c, 6b)) from the Coniacian of Wyoming.

*P. (Protexanites) strozzii* (Desio) (1920: 204, pl. 12(1) (fig. 8)) from the Senonian of Florence, Italy.

To this list may be added:

*P. (Protexanites) eugnamtus* (Redtenbacher) (1873: 117, pl. 27 (fig. 1a–c)) from the Coniacian of the Gosau Beds, Austria. (See Reyment 1958: 45.)

Of these species half are either monotypic or poorly known, having been figured once or twice only. These include *P. (P.) canaensis* and its variety *obliquecostata*, *P. (P.) peroni*, *P. (P.) strozzii* and *P. (P.) eugnamtus*.

Detailed descriptions and figures to illustrate the extensive intraspecific variation and ontogeny of *P. (P.) shoshonense* and *P. (P.) planatus* were provided by Reeside (1927) and Young (1963) respectively. Illustrations and descriptions of the types of *P. (P.) bourgeoisi* and *P. (P.) bontanti* were provided by Matsumoto (1966, 1970).

As appears to be the case in other regions, *Protexanites* is poorly represented in the Coniacian of Zululand, both in numbers and in species. One species only, *P. (P.) cycni* (van Hoepen) is described below.

Due to their relative scarcity throughout the world, current systematics in *Protexanites* seems to be typologic, rather than based on actual populations, and is extremely conservative when compared with systematic concepts applied to *Texanites* or *Submortonicerases*. Specific characters in *Protexanites* include, apart from relative proportions, density and curvature of ribbing, strength and position of the umbilical (1) and submarginal (3) tubercle, and whether the keel is entire or crenulate. Amongst these, possibly only the latter is of real significance in *Texanites*, but it varies according to preservation.



Comments on the phylogeny of *Protexanites* and *Paratexanites* are given on p. 16.

### Occurrence

Coniacian to Lower Santonian of western and central Europe (France, Spain, Italy, Austria, Czechoslovakia, Rumania), Israel and Sinai, North America (Gulf Coast and Western Interior), South America (Venezuela and Peru), Japan and Saghalien, north Africa (Algeria), South Africa (Zulu-land), and Madagascar.

### *Protexanites (Protexanites) cyni* (van Hoepen, 1965)

Figs 2-4

*Subprionocyclus cyni* van Hoepen 1965b: 183, plate I.

*Subprionocyclus cyni?* van Hoepen 1965b: 183.

### Type

Holotype is SAS-Z651 by the original designation of Van Hoepen (1965b: 183), here refigured as Figure 2D-F.

### Material

SAS-Z808 and SAS-Z832, locality 93, near the Hluhluwe Estuary, Zululand, St Lucia Formation, Coniacian II to possibly III, the same locality and horizon as the holotype; BMNH-C81431-C81433, locality 91, close by locality 93, St Lucia Formation, Coniacian IV-V.

### Dimensions

|      | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|------|----------|------------|------------|----------------|------------|-------------|-------------|
| Z651 | 43,0     | 13,0(30)   | 17,0(40)   | 0,76           | 14,0(33,0) | —           | —           |
| Z834 | 62,0     | 20,0(32,3) | 21,5(34,7) | 0,93           | 26,0(41,9) | 16          | 22          |
| Z832 | 72,0     | —          | 28,0(38,9) | —              | 28,0(38,9) | 7×2         | 15×2        |
| Z808 | 90,0     | 27,0(30,0) | 32,0(35,5) | 0,84           | 37,0(41,1) | 9×2         | 12×2        |

### Description

This is a relatively small-shelled species, the maximum observed diameter being 102 mm, of which half is body chamber. The umbilical width varies during ontogeny, being narrowest in early stages at 33 per cent, to wide in later stages at 41 per cent. Whorl overlap is negligible. Barring the early, smooth stage, the whorl section throughout is higher than wide, with maximum width at the umbilical edge (Fig. 3E). The umbilical wall is high, nearly vertical to overhanging, and the flanks little inflated, converging to a flattened venter. Towards the body chamber the section becomes a little more inflated. The ventral keel is very prominent, with weak serrations, corresponding in number to lateral ornament.

Ornament basically consists of radially pinched, sometimes overhanging prominent umbilical (1) tubercles connected to stout, spirally elongated sub-

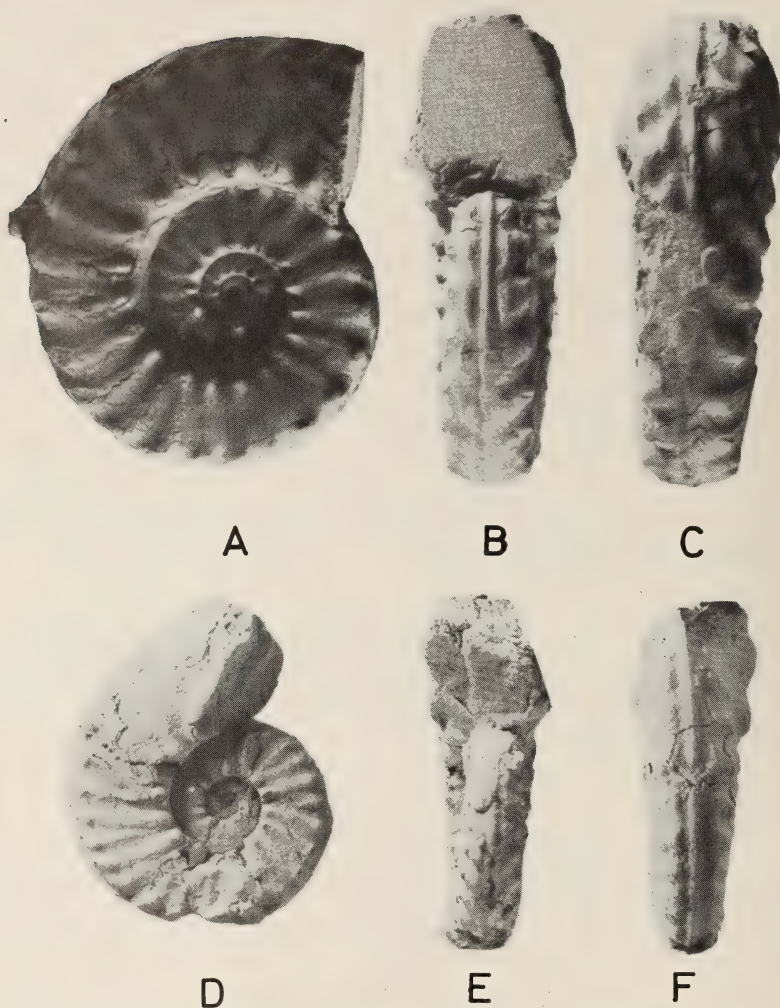


Fig. 2. *Protexanites (Protexanites) cycni* (van Hoepen, 1965). A-C. SAS-Z834. D-F. Holotype SAS-Z651.  $\times 1$ .

marginal (3) tubercles by means of low, fold-like, finely striate and virtually straight ribs which occasionally bifurcate at the umbilical tubercles. Indistinct intercalatories also occur, resulting in more submarginal (3) and external (5) tubercles than umbilical ones. The external (5) tubercles are very thin and spirally elongated and situated slightly forward of the submarginal (3) ones. The distance between these latter two rows is very small, and in early stages of growth they are connected by low, broad fold-like ribs. On the holotype, the external (5) tubercles appear as a discontinuous, wavy lateral keel.



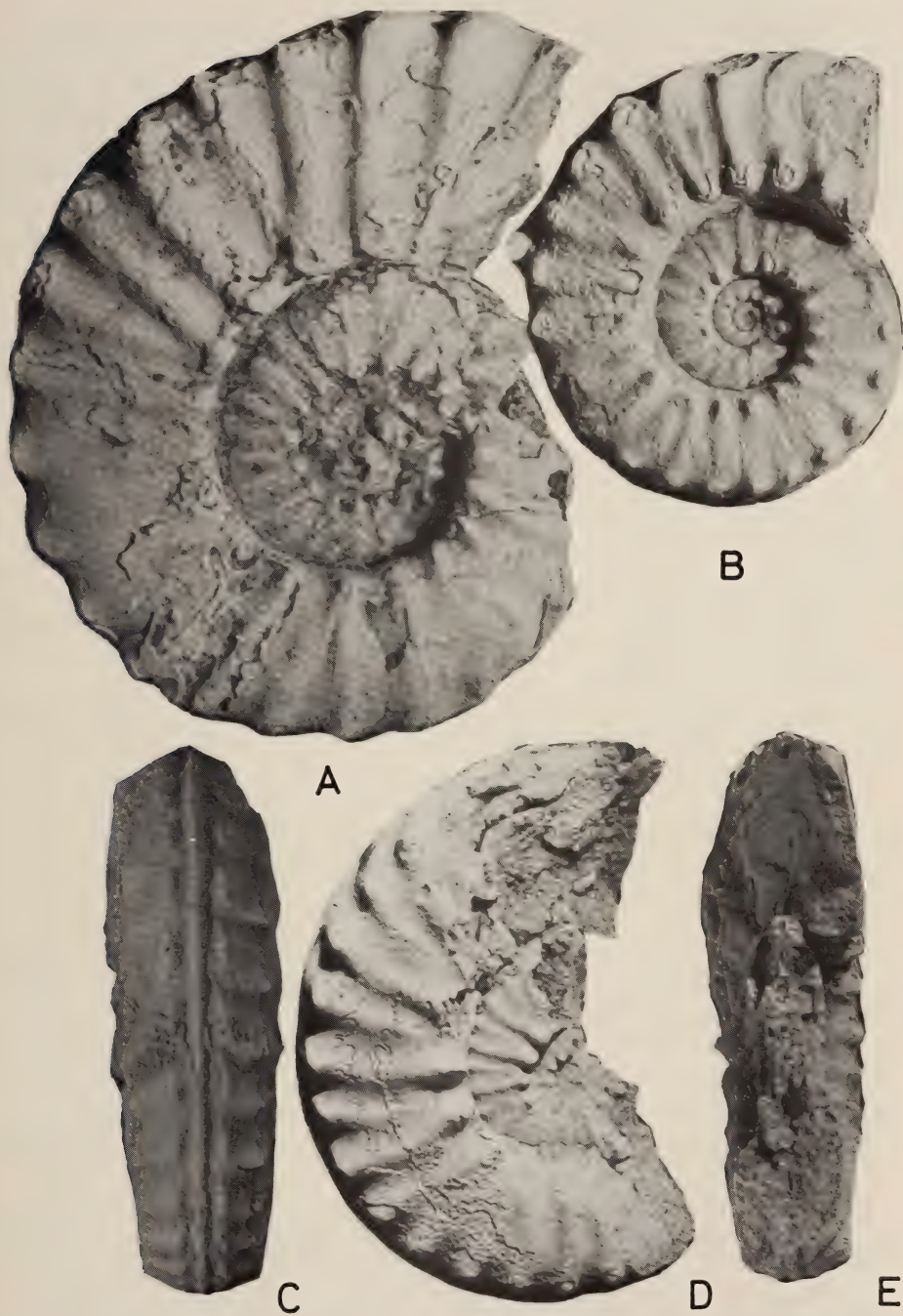


Fig. 3. *Protexanites (Protexanites) cyni* (van Hoepen, 1965. A. SAS-Z808. B. SAS-Z834. C-E. SAS-Z832. A, C-E  $\times 1$ ; B  $\times 1,1$ .

SAS-Z834 shows details of the ontogeny (Figs 2A-C, 3B). On the innermost whorls, up to a diameter of *c.* 6 mm, the whorls are rounded and devoid of visible ornament. Beyond that diameter, umbilical (1) tubercles and very weak, bifurcating fold-like ribs start appearing. Microscopic examination of the ribs shows them to be ornamented by numerous radial striae. With the onset of ornament, the whorl section changes and becomes rectangular. Traces of the submarginal (3) tubercles become visible in the umbilical seam at a diameter of about 14 mm. From then onward, ornament remains basically the same, apart from the fact that the ribs tend to become more prominent on the body chamber.

The external suture is relatively simple with a broad, asymmetrically bifid lateral lobe (Fig. 4).



Fig. 4. *Protexanites* (*Protexanites*) *cycni* (van Hoepen, 1965). Suture line of SAS-Z832. Scale bar in millimetres.

### Discussion

The main characteristics of this species are the subrectangular whorl section with little-inflated flanks, ornamented by weak, flattened ribs with occasional bifurcations and intercalations and by the weakly crenulate keel.

Van Hoepen (1965*b*: 183) based this species on an immature juvenile specimen, still fully septate at the largest diameter. On the basis of the present material, the authors would place this specimen in *Protexanites* rather than in *Subprionocyclus*, as suggested by Van Hoepen, although the dividing line between the two taxa here becomes indistinct.

As far as the crenulate keel is concerned, comparisons may be drawn with *P. (P.) bourgeoisi* and *P. (P.) bontanti bontanti*. Both species were recently reviewed on the basis of the original material by Matsumoto (1966, 1970). *P. (P.) bourgeoisi* has more sinuous ribs than *P. (P.) cycni* and exhibits a tendency for the umbilical tubercles to migrate away from the umbilical wall up the flanks, quite unlike those of *P. (P.) cycni*.



*P. (P.) bontanti* s.s. in the sense of Matsumoto (1970: 235–237) has a narrower umbilical diameter (31–33%) than *P. (P.) cycni*, and denser, more flexuous ribbing. The whorl sections, however, are comparable apart from slight differences in whorl height, possibly indicating genetic affinity. *P. (P.) bontanti shimizui* was erected by Matsumoto (1970: 237) (see also Matsumoto & Hirano 1976: 335) for a subspecies differing from the nominate subspecies in possessing an entire ventral keel which is as high as the external tubercles. In this respect *P. (P.) bontanti shimizui* is easily distinguished from *P. (P.) cycni*. Matsumoto (1970: 235–237) discussed the affinities of *P. (P.) bontanti* s.s., and little can be added apart from comment on the specimens figured by De Grossouvre (1894, pl. 17 (figs 2–3)). The specimen figured by De Grossouvre (1894, pl. 17 (fig. 3)) does not belong to *P. (P.) bontanti* s.s. because of the presence of a fourth row of tubercles on the dorsal part of the flanks on the outer whorl. This may be an example of *P. (Anatexanites)*.

Comparisons with other *Protexanites* s.s. species are as follows:

*P. (P.) canaensis* (Gerhardt) does not have as strongly developed umbilical tubercles and is generally more weakly ornamented with a more rectangular whorl section.

*P. (P.) peroni* Matsumoto has more flexuous ornament and apparently lacks, or has very few, bifurcating ribs on the outer whorls.

*P. (P.) planatus* (Lasswitz) has much coarser ornament throughout.

In *P. (P.) shoshonensis* (Meek), as in *P. (P.) bourgeoisi*, the umbilical tubercles tend to migrate away from the umbilical wall up the flanks.

*P. (P.) strozzii* (Desio) is difficult to interpret, but seems to have more flexuous ornament on the outer whorl, although the inner whorls are comparable with those of *P. (P.) cycni*.

*P. (P.) eugnamtus* (Redtenbacher) has coarse, but very closely-spaced ornament, clearly differing from *P. (P.) cycni*.

#### Occurrence

Coniacian II to possibly V of Zululand.

Genus *Paratexanites* Collignon, 1948

(= *Parabevahites* Collignon, 1948)

#### Type species

*Mortoniceras zeilleri* de Grossouvre, 1894, by the original designation of Collignon (1948: 45).

#### Diagnosis

The size of the shell is variable. Ornament consists of predominantly single ribs, each bearing four rows of tubercles in the adult stage; umbilical (1), submarginal (3), marginal (4), and external (5). In early stages the submarginal (3) and marginal (4) tubercles are situated close together, sharing a single base. Separation of these two tubercles takes place at varying diameters, and in some

specimens presumably not at all. The marginal (4) tubercle develops by splitting from the submarginal (3) one. The keel may be entire or undulating. Faint indications of lateral keels joining the external (5) tubercles may occur in some species.

### Discussion

Wright (1957: L431-432) and Matsumoto (1970: 248) recognized two subgenera:

*Paratexanites* (*Paratexanites*) (type species *Mortonicerias zeilleri* de Grossouvre 1894).

*Paratexanites* (*Parabevahites*) (type species *Ammonites serrato-marginatus* Redtenbacher, 1873).

The main differences between the two subgenera are that in *Paratexanites* s.s. the submarginal (3) and marginal (4) tubercles become separated, whereas in *P. (Parabevahites)* they remain approximated, presumably also on the outer whorls.

The Zululand material shows that it is difficult to decide when the two rows of tubercles have separated sufficiently to be referred to *Paratexanites* s.s., rather than being retained in *P. (Parabevahites)*. This criterion is extremely ambiguous, and seems impossible to apply satisfactorily to the material: it probably reflects ontogenetic rather than specific differences. Similar doubts on this matter were also expressed by Young (1963: 80). The only species which seem to retain the two rows of tubercles close together to great diameters are the type species, *Ammonites serrato-marginatus*, *Ammonites emscheris* Schlüter, and *Parabevahites sellardsi* Young. Of these species, the first two are poorly defined and enigmatic (see Matsumoto 1970: 249 and herein p. 15). Only *P. sellardsi* is based on sufficient material to gain some idea as to intraspecific variation.

In consequence, it is here considered that retention of *Parabevahites* is probably unnecessary, and that it is better placed in the strict synonymy of *Paratexanites* s.s.

Thus defined, species known to be referred to *Paratexanites* are:

*Paratexanites compressus* Matsumoto (1970: 255, pl. 36 (figs 4-5), text-fig. 13) from the Santonian of Hokkaido.

?*Paratexanites desmondi* (de Grossouvre) (1894: 79) from the Coniacian or Santonian of France.

*Paratexanites emscheris* (Schlüter) (1876: 41, pl. 42 (figs 8-10)) from the Coniacian of northern Germany.

*Paratexanites muramotoi* Matsumoto (1970: 257, pl. 37 (fig. 1), text-fig. 14)) from the Coniacian of Hokkaido.

*Paratexanites orientale* (Yabe) (Yabe & Shimizu 1925: 129, pl. 31 (figs 4-5), pl. 33 (fig. 16)) from the Upper Coniacian of Hokkaido.



*Paratexanites rex* Matsumoto (1970: 249, text-fig. 9(83)) (= *Ammonites texanus* in Schlüter 1876: 41, pl. 12 (figs 1–3)) from the glauconitic marls of Stoppenberg, Germany.

*Paratexanites serratomarginatus* (Redtenbacher) (1873: 110, pl. 25 (fig. 2a–d)) from the Coniacian of Austria, France and Japan, and, doubtfully, Madagascar and Zululand.

*Paratexanites sellardsi* Young (1963: 79, pl. 32 (fig. 7), pl. 36 (figs 3–5), pl. 37 (fig. 1), pl. 39 (fig. 4), pl. 49 (fig. 3), text-fig. 17) from the Upper Coniacian of the Gulf Coast of North America.

*Paratexanites zeilleri* (de Grossouvre) (1894: 67, pl. 14 (fig. 1)) from the base of the Craie de Villedieu, France.

*Paratexanites umkwelanense* (Crick) (1907: 228, pl. 15, (fig. 9–9a)) from the Upper Coniacian to Lower Santonian of Zululand.

*Paratexanites mikasaensis* Matsumoto (1970: 258, pl. 37 (figs 2–3), text-fig. 15) from an indefinite horizon of Upper Coniacian to Lower Santonian age in Hokkaido.

*Paratexanites collignoni* (Fabre-Taxy) (1963: 19, pl. 1 (fig. 11)) from the Lower Santonian in France.

Matsumoto (1970) recently discussed the scope of the genus, and few comments only are needed on some of the above listed species.

*P. zeilleri* is monotypic. The German specimen included in the synonymy of *P. zeilleri* by De Grossouvre (*Ammonites texanus* in Schlüter 1867: 32 *pars*, pl. 6 (fig. 1a–b) only) is a specimen of *Texanites*, according to Matsumoto (1970: 249).

*P. desmondi* was erected by De Grossouvre (1894: 79) without providing a figure. De Grossouvre included one of Schlüter's (1867, pl. 6 (fig. 3)) specimens of *Ammonites texanus* in *P. desmondi*, but this specimen is to be regarded as an inner whorl of *P. rex* rather than *P. desmondi*, according to Matsumoto (1970: 251). De Grossouvre's description of *P. desmondi* is based on a fragment of a whorl, with the first row of tubercles on the first third of the whorls, the second on the second third of the whorl, and the third and fourth, which are rounded, close together on the venter. The authors follow Collignon (1948: 72) in leaving interpretation of the species open to doubt until the specimen is properly illustrated.

*P. emscheris* is based on a fragment of an outer whorl, and is difficult to interpret. This led De Grossouvre to include the species in the synonymy of *P. serratomarginatus*, a view not supported here. *P. emscheris*, at any rate, retains the *Parabevahites* row of doubled tubercles to a large diameter.

*P. serratomarginatus* is enigmatic. Redtenbacher based the species on seven specimens, of which two were figured, an immature septate individual and a body chamber fragment. The specimen figured by De Grossouvre (1894, pl. 16 (fig. 1a–b)) is still septate at a much larger diameter than Redtenbacher's larger figured specimen, and has coarser ornament. According to Matsumoto (1970:

263) De Grossouvre's specimen merits separation at subspecific level as *P. serratomarginatus grossouvrei*.

*P. rex* was erected by Matsumoto (1970: 249) for a specimen originally identified as *Ammonites texanus* by Schlüter (1872: 41 *pars*, pl. 12 (figs 1–3)), but subsequently referred to *P. emscheris* by the latter (Schlüter 1876: 155).

The specimen from Madagascar described as *Parabevahites dubius* by Collignon (1966a: 133, pl. 513 (fig. 2026)) has a distinct lateral tubercle, and the submarginal (3), marginal (4), and external (5) tubercles situated close together on an elevation in *Parabevahites* fashion. The species is most probably to be referred to *Plesiotexanites*. Similarly *Parabevahites? transitorius* Collignon (1966a: 80, pl. 488 (fig. 1970)), with *Parabevahites*-like inner whorls but pentatuberculate outer whorls, is to be referred to *Plesiotexanites*.

Species of *Paratexanites* are locally abundant in the Upper Conacian to Lower Santonian sediments in the floodplains of the Mzinene and Hluhluwe Rivers in Zululand, and provide important data on the phylogeny of the Texanitinae.

The species to be described from Zululand are:

*P. australis* sp. nov.

*P. pseudotricarinatum* sp. nov.

*P. umkwelanense* (Crick)

*P. sp. aff. P. emscheris* (Schlüter)

*P. sp. aff. P. serratomarginatus* (Redtenbacher)

According to current opinion, the origin of *Paratexanites* should be sought in *Protexanites*. Young (1963: 79) drew attention to similarities between *Paratexanites zeilleri* and *Protexanites bourgeoisi*, and *Paratexanites sellardsi* and *Protexanites planatus* respectively, while Matsumoto (1970: 252) pointed to similarities between *Paratexanites compressus* and *Protexanites bontanti*, and *Paratexanites mikasaensis* and *Protexanites canaensis* respectively. Available stratigraphic data, however, show that some of these *Protexanites* and *Paratexanites* species occur together at the same stratigraphic level, or that *Protexanites* may be even younger than *Paratexanites* locally.

The earliest known *Paratexanites* species in Zululand, *P. australis* sp. nov., is transitional between *Protexanites* and *Paratexanites* in remaining trituberculate to a large diameter. As yet, however, no true *Protexanites* is known connecting to *Paratexanites australis* sp. nov. Available data in Zululand suggest that *P. australis* sp. nov. is derived from the aberrant peroniceratid '*Fraudatoroceras*' *besairiei* van Hoepen, 1965b (Figs 5–7, 16A–C) with simple collignoniceratid sutures. There probably was a *Protexanites* transitional stage between '*Fraudatoroceras*' *besairiei* and *Paratexanites australis* sp. nov. as shown below (p. 29).

This raises the possibility that *Protexanites* and *Paratexanites* may be diphyletic as here interpreted. Matsumoto (1970: 230) suggested that *Protexanites* could be derived from *Subprionocyclus*. In relatively weakly orna-



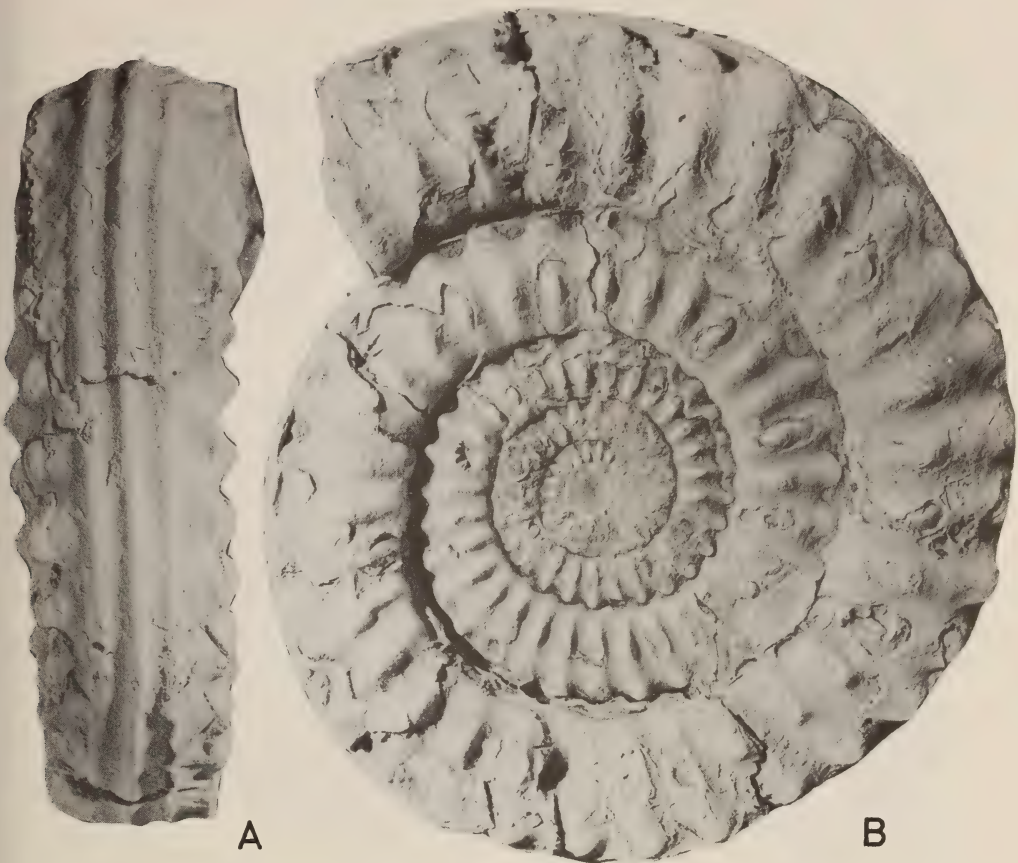


Fig. 5. '*Fraudatoroceras*' *besairiei* van Hoepen, 1965. Holotype SAS-Z756, the specimen figured by Van Hoepen 1965 as plate 27, but lacking the outer septate whorl.  $\times 0,95$ .

mented species such as *P. (P.) bontanti*, *P. (P.) canaensis* and *P. (P.) cycni*, this line of descent seems feasible, whereas the stronger ornamented species, such as *P. (P.) bourgeoisi*, *P. (P.) shoshonense*, and *Paratexanites australis* sp. nov., appear closer to '*Fraudatoroceras*' *besairiei*. On the basis of the present evidence a division of *Protexanites* and *Paratexanites* along these lines would be impracticable. In addition, *P. australis* sp. nov. shows occasional traces of multiplication of the external tubercles, and corresponding nodes on the keel, very reminiscent of *Protexanites* (*Pleurotexanites*), differing only in having a doubled ventrolateral tubercle. This could again possibly be the origin of *Bevahites*.

*Plesiotechanites*, which in younger stages has a *Paratexanites*-like arrangement of the submarginal (3), marginal (4), and external (5) rows of tubercles, may be derived from *Paratexanites* through addition of the lateral tubercle. The holotype of *Paratexanites pseudotricarinatum* sp. nov. already shows faint traces of a lateral tubercle, foreshadowing the development of *Plesiotechanites*.

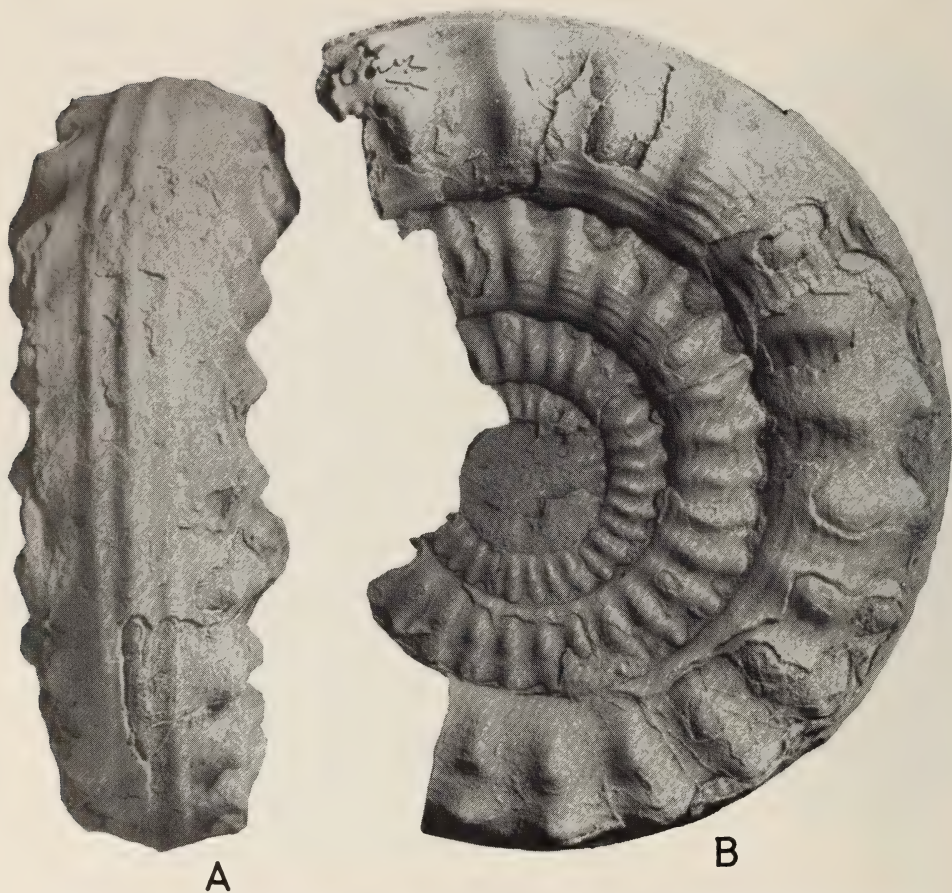


Fig. 6. '*Fraudatoroceras*' *besairiei* van Hoepen, 1965. SAS-Z1522, with more prominent lateral ornament than the holotype, and distinct concentric striae.  $\times 1$ .



Fig. 7. '*Fraudatoroceras*' *besairiei* van Hoepen, 1965. Holotype SAS-Z756, showing suture line; after Van Hoepen (1965: 32, fig. 9a).  $\times 1$ .



*Occurrence*

*Paratexanites* occurs in the Coniacian to Santonian of western and central Europe, north Africa and South Africa, Madagascar, North America, and Japan.

*Paratexanites australis* sp. nov.

Figs 8–15, 16D–F

*Holotype*

SAS-Z1121 (Fig. 8), locality 73, lower reaches of the Mzinene River, Zululand, St Lucia Formation, Coniacian IV–V to Santonian I.

*Etymology*

Refers to occurrence in southern Africa.

*Material*

Paratypes are NMB-D1060a–b, from the same locality as the holotype; SAS-H148/2, locality 14, a small quarry east of Riverview Sugarmill, St Lucia Formation, Coniacian IV; SAS-Z180, SAS-Z186, and SAS-H75c, from an unknown locality near the Hluhluwe River estuary, probably locality 89–91, St Lucia Formation, Coniacian IV–V; and BMNH-C81434–5, locality 88, same Formation and age.

*Dimensions*

|        | D     | Wb         | Wh         | Wb : Wh | U          | Int.   | Ext.   |
|--------|-------|------------|------------|---------|------------|--------|--------|
| Z1121  | 83,0  | 31,0(37,3) | 28,0(33,7) | 1,11    | 37,0(44,6) | 20     | 20     |
| Z180   | 77,0  | 31,0(47,3) | 27,0(35,1) | 1,15    | 32,0(41,6) | 10 × 2 | 10 × 2 |
| H148/2 | 70,0  | 29,0(41,4) | 27,0(38,6) | 1,07    | 28,5(40,7) | 12 × 2 | 12 × 2 |
| Z186   | 123,0 | 38,0(30,9) | 46,0(37,4) | 0,82    | 54,0(43,9) | 23     | 25     |

*Description*

The shell is relatively small; maximum diameter observed is 123 mm. Coiling is very evolute, with a shallow dorsal zone of impression and an umbilical width of the order of 40 to 45 per cent. The whorl section varies with ontogeny (Fig. 15B–C), changing from depressed rectangular in the greater part of the phragmocone, to square on the later part, to compressed on the body chamber.

Details of ontogeny can be observed in H148/2 (Figs 9–10) and SAM-PCZ5901 (Fig. 11D–E). The whorls are smooth up to a diameter of 4 mm, thereafter low ribs start appearing, with prominent ventrolateral tubercles, leaning or impressed into the umbilical wall of the succeeding whorl in H148/2 (Fig. 9). Umbilical tubercles start appearing at a diameter of 6,5 mm in H148/2, and at 10 mm the umbilical edge is well defined, thus giving the whorl the rectangular section characteristic of the species. The venter at this stage is fastigiate with a distinct ventral keel and very indistinct lateral keels (Fig. 11D–E). With increasing diameter at c. 12 mm, the ventrolateral tubercles

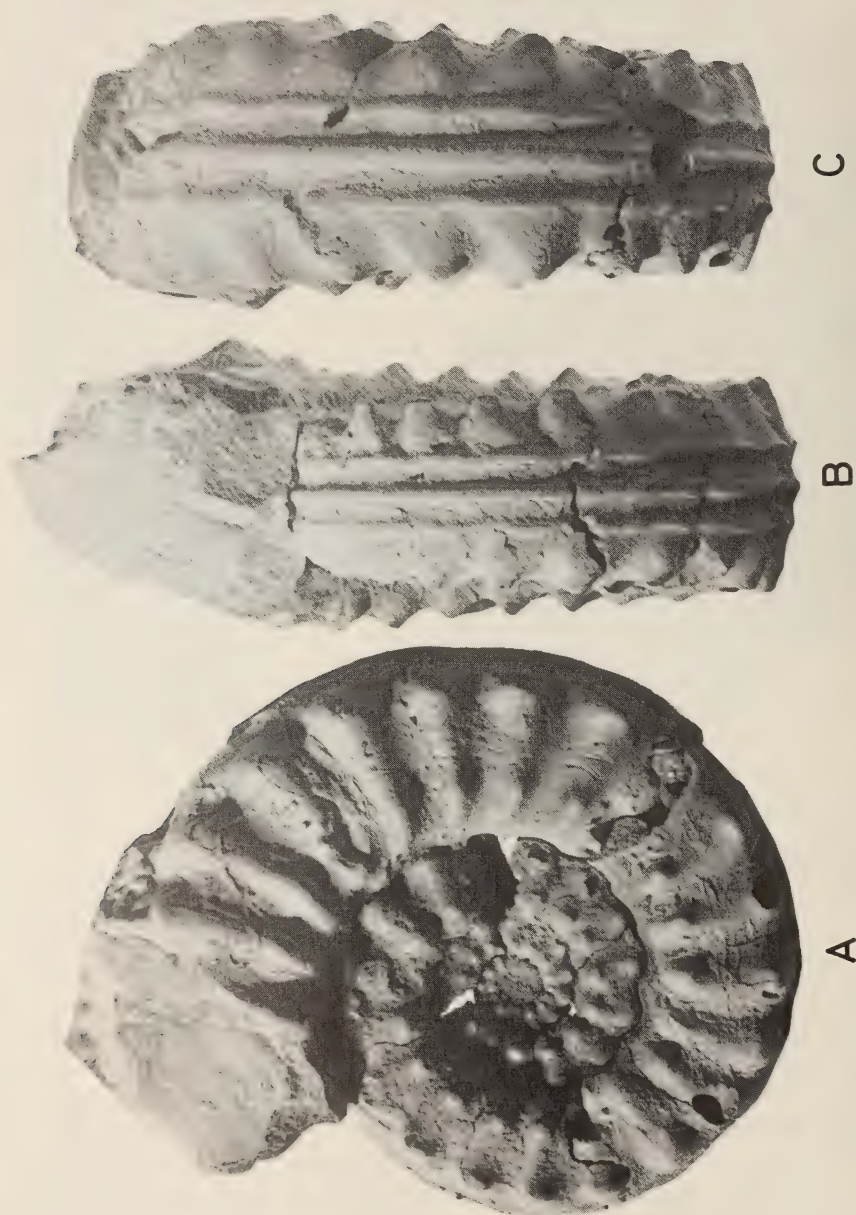


Fig. 8. *Paratexanites australis* sp. nov. Holotype SAS-Z1121. Note the elongated external tubercles forming wavy lateral keels, similar to '*Fraudatoroceras besairiei*'.  $\times 1$ .





Fig. 9. *Paratexanites australis* sp. nov. Paratype SAS-Z148/2. Note the initial smooth inner stage, followed by pointed ventrolateral and eventually conical umbilical and long spinose ventrolateral tubercles. Scale bar in millimetres.

become forwardly projected over the venter, foreshadowing the development of the external row of tubercles.

Ornament now consists of conical to radially elongated umbilical tubercles, pointing laterally, connected by single, low and broad, often concave ribs to well-developed rounded to spinose ventrolateral tubercles. The umbilical tubercles are situated at the umbilical edge or are displaced slightly ventrally. The external tubercles are poorly developed and appear as wavy lateral keels.



Fig. 10. *Paratexanites australis* sp. nov. Paratype SAS-H148/2. Note the distinctly separated external tubercles.  $\times 1$ .



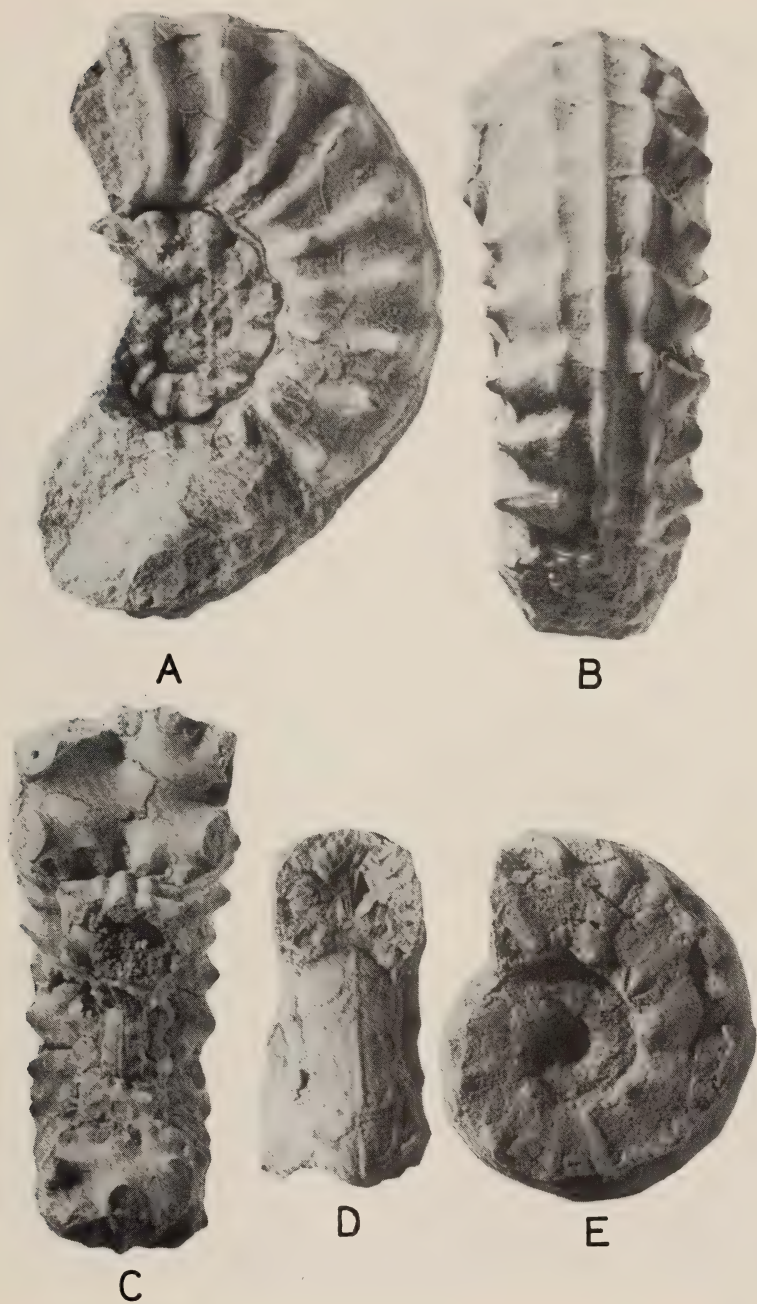


Fig. 11. *Paratexanites australis* sp. nov. A-B. Paratype NMB-D1060 with undulating lateral keel. C. Holotype SAS-Z1121 before repair. D-E. Inner whorls of paratype SAM-PCZ5901 to show early ornament and pseudotricarinate venter. A-C  $\times 1$ ; D-E  $\times 3.9$ .

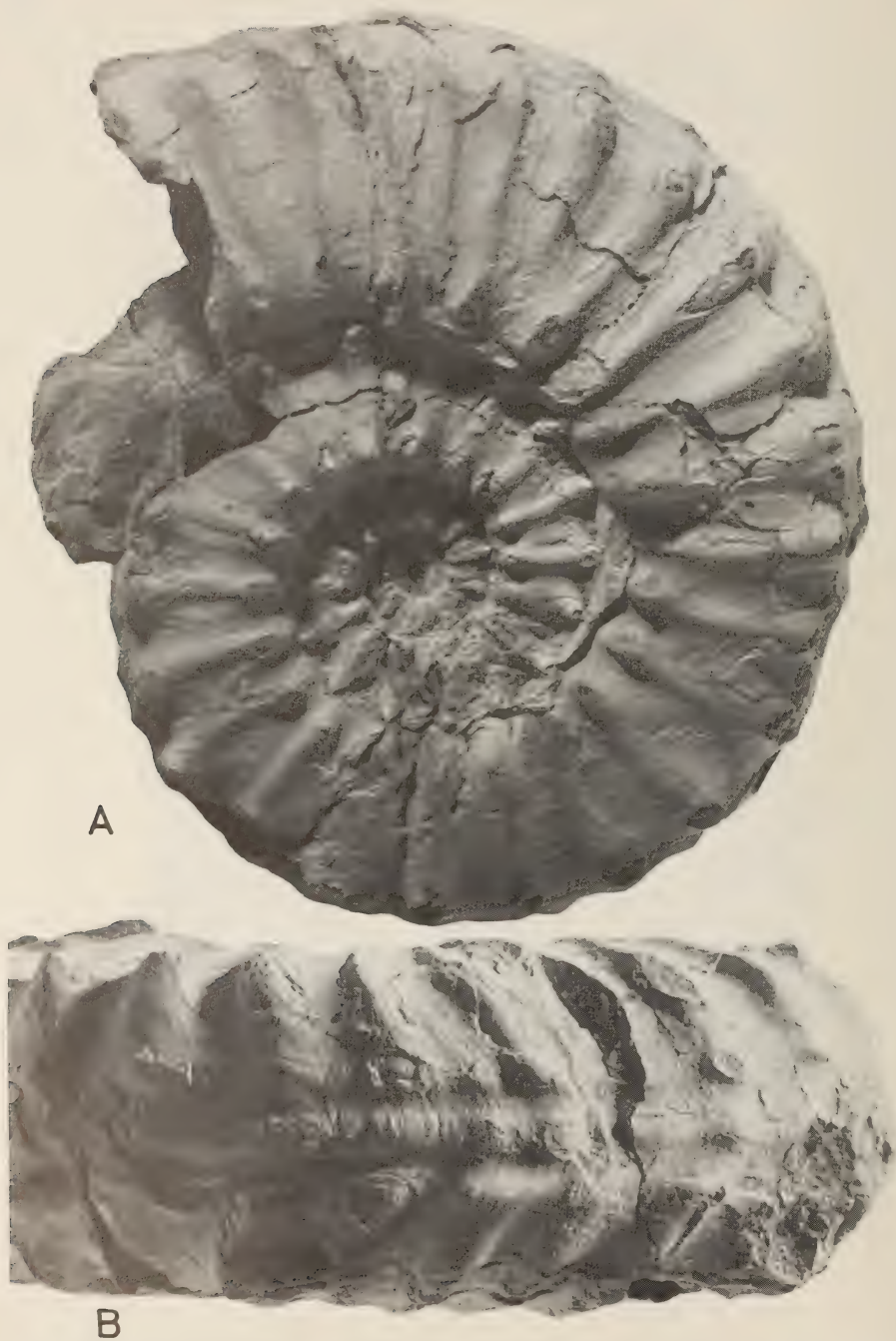


Fig. 12. *Paratexanites australis* sp. nov. Paratype SAS-Z186. B illustrates the local multiplication of external tubercles on the venter of part of the phragmocone.  $\times 1$ .





Fig. 13. *Paratexanites australis* sp. nov. Paratype SAS-Z186.  $\times 1$ .

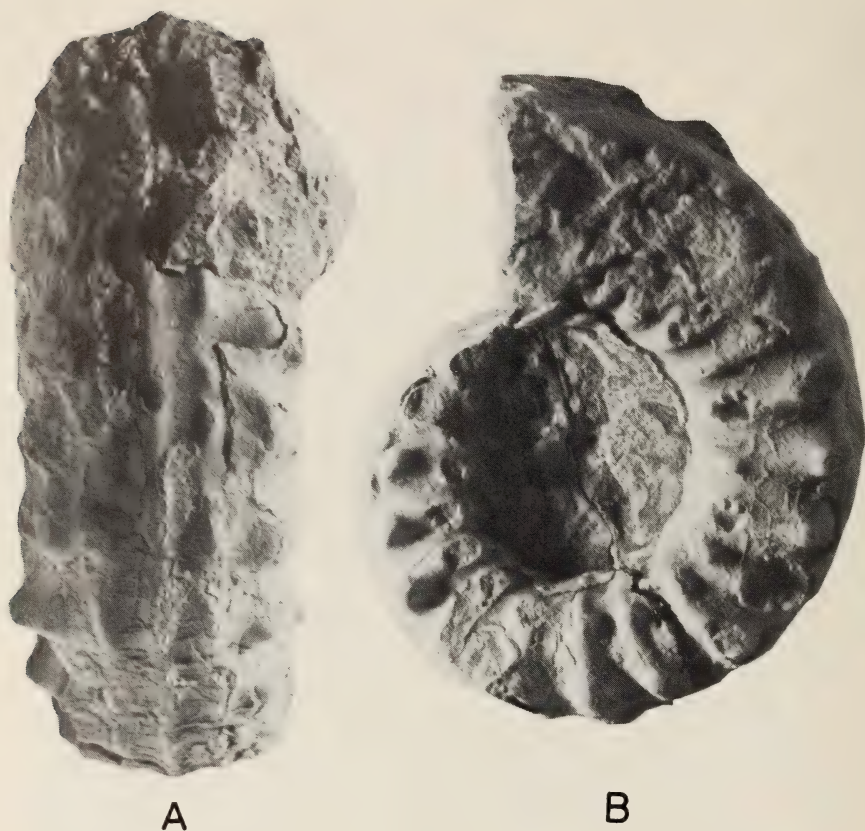


Fig. 14. *Paratexanites australis* sp. nov. Paratype SAS-Z180. A illustrates local multiplication of external tubercles on the venter of part of the phragmocone.  $\times 1$ .

Beyond this trituberculate stage ornament in the material varies considerably. The ventrolateral tubercles tend to become lower and broader, and in some of the specimens (e.g. SAS-H75c, SAS-Z180, and NMB-D1060a) (Figs 11A-B, 14) the formation of two distinct ventrolateral rows of tubercles takes place, though still united by a single, common broad base. In SAS-Z186 (Figs 12-13) no distinct separation takes place and the specimen remains trituberculate throughout. Similar differences are to be found in the ventral ornament. The external tubercles may appear as two lateral keels as in SAS-H75c, through slightly wavy discontinuous lateral keels as in SAS-Z1121 (Fig. 8), to distinct, though very elongated, clavi as in SAS-H148/2 (Fig. 10). The central keel is wavy throughout and higher than the external tubercles (or undulating lateral pseudo-keels). In places, the undulations on the keel are so strong as to appear as a central row of tubercles. Furthermore, in specimens SAS-Z186 (Fig. 12B) and Z180 (Fig. 14A) multiplication of the external tubercles and corresponding undulations on the keel takes place locally. Lateral ornament



continues weakly over the venter in places, creating, together with the undulating lateral keels, a reticulate pattern over the venter (Fig. 13).

In SAS-Z186 (Fig. 12A) ornament weakens on the body chamber, and two bifurcating ribs are present.

The suture line is rather variable as far as complexity of incision of the elements and width of saddles is concerned, tending to be more complex than in later collignoniceratid species (Fig. 15A).

#### Discussion

The species is here interpreted widely, but is identified mainly by the depressed rectangular whorl section in the greater part of the phragmocone, the prominent ornament and the late, or suppressed, division of the ventro-lateral tubercles.

In the latter respect (i.e. late or indistinct appearance of quadrituberculate stage), the species appears to be morphological intermediate between *Protexanites* s.s. and *Paratexanites*. However, the only Zululand representative of *Protexanites*, *P. cyni*, has completely different morphological features, and seems to bear very little genetic relation.

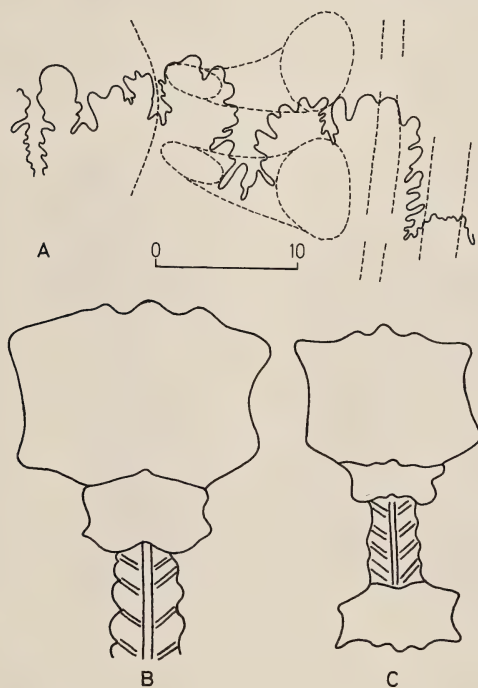


Fig. 15. *Paratexanites australis* sp. nov. A. Suture line of SAS-Z1121. B-C. Whorl section of early stages of SAS-Z1120 and SAS-Z1121 respectively. Scale bar in millimetres.

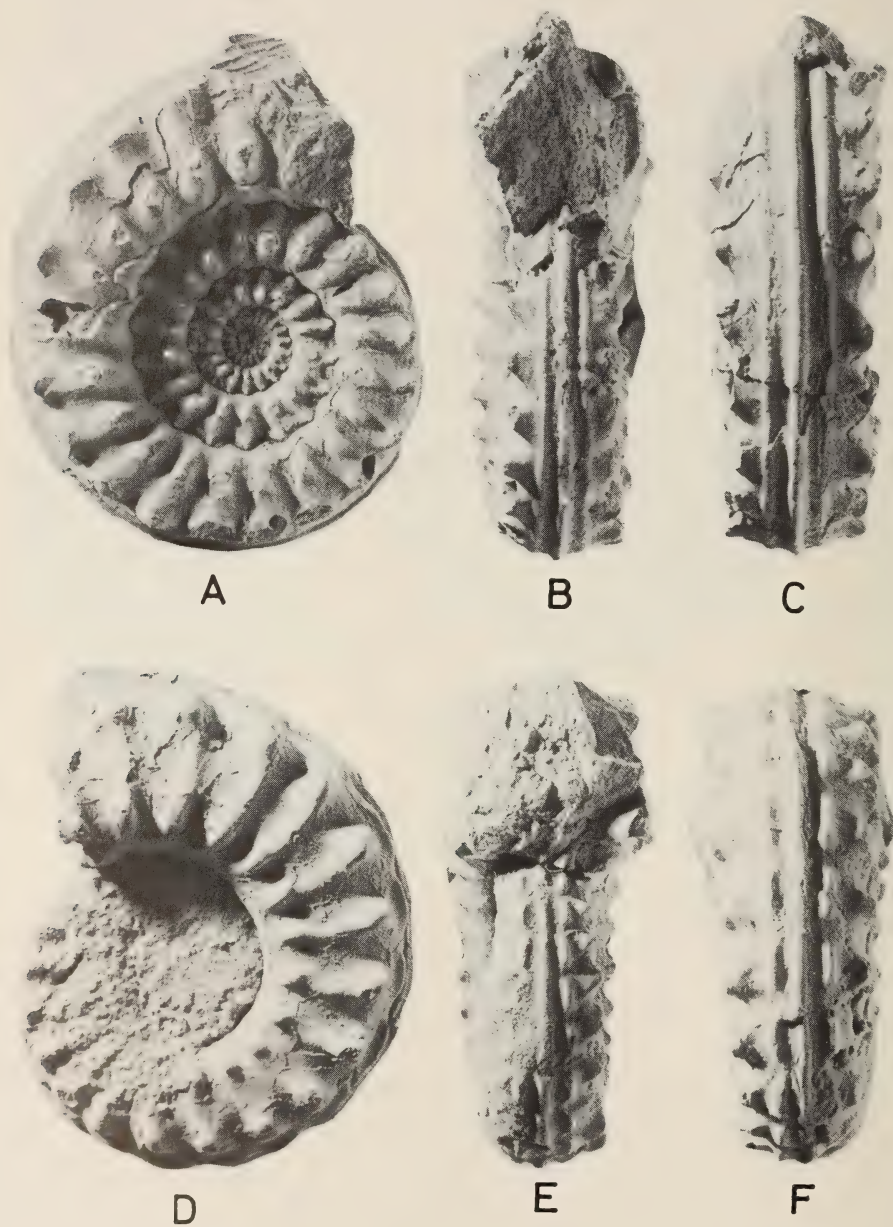


Fig. 16. A-C. '*Fraudatoroceras*' *besairiei* van Hoepen, 1965. SAS-Z1120a. D-F. *Paratexanites australis* sp. nov. Paratype NMB-D1060b. The figure illustrates the similarity between the aberrant peroniceratid '*Fraudatoroceras*' *besairiei* and *Paratexanites australis* sp. nov.  $\times 1$ .



As far as overall morphology and relative complexity of the suture line is concerned, the closest allied species is the tricarinate peroniceratid '*Fraudatoroceras*' *besairiei* van Hoepen (1965a: 36, pl. 27) (Figs 5-9, 16A-C) which occurs at a slightly lower stratigraphic level. The latter has a similar depressed whorl section on the phragmocone, and comparable ornament consisting of radially elongated umbilical tubercles, single, slightly concave ribs and prominent clavate ventrolateral tubercles. Through reduction of the umbilical width, crenulation of the keel, separation of the lateral keels into external tubercles and splitting of the ventrolateral tubercles, *Paratexanites australis* may be derived from '*Fraudatoroceras*' *besairiei* van Hoepen. As described above, the present specimens display considerable variation in respect of these characteristics, thus providing transitional forms between '*Fraudatoroceras*' and *Paratexanites*. SAS-Z186 (Figs 12-13), which apparently retains the trituberculate stage throughout, provides the *Protexanites* stage connecting between '*Fraudatoroceras*' and *Paratexanites australis*. Two juvenile specimens, SAS-Z1120a (Fig. 16A-C) and NMB-D1060b (Fig. 16D-F), show the great similarity between '*Fraudatoroceras*' *besairiei* and *Paratexanites australis*, the only difference being the presence of an entire lateral keel in the former compared to a row of long, nearly touching external tubercles.

Apart from providing a link between the Texanitinae and Peroniceratinae, *P. australis* sp. nov. may also possibly provide material for derivation of *Plesiotexanites*, *Protexanites* (*Pleurotexanites*) and other species of *Paratexanites*: the inner whorls are remarkably similar to those of *Plesiotexanites matsumotoi* sp. nov. to be described below from the Middle Santonian part of the Umzamba Formation.

The occasional multiplication of the external tubercles, and corresponding elevations on the central keel may perhaps be regarded as the forerunner of the condition as found in *Protexanites* (*Pleurotexanites*) *superbus* (Collignon) from which *Bevahites* and, possibly, *Menabites* may be derived.

*Paratexanites umkwelanense* (Crick) and *Paratexanites pseudotricarinatum* sp. nov. to be described below (p. 44) may also be derived either directly from *P. australis* sp. nov., or from a common source.

As far as whorl section and late appearance of the trituberculate stage is concerned, the closest ally to *P. australis* seems to be *P. orientalis* (Yabe). In this latter species, however, separation of the marginal and submarginal tubercles is complete, and it would seem to fit a morphological position between *P. australis* sp. nov. and *P. umkwelanense* (Crick).

### Occurrence

Upper Coniacian to possibly Lower Santonian of Zululand.

*Paratexanites umkwelanense* (Crick, 1907)

Figs 17–20A, 21–30

*Mortoniceras umkwelanense* Crick, 1907: 228, pl. 15 (fig. 9–9a).*Non Mortoniceras* aff. *umkwelanense* Spath, 1921: 234, text-fig. D2.*Paratexanites umkwelanensis* Matsumoto, 1955: 41, text-fig. 2.*Type*

The holotype is BMNH C18134 from Umkwelane Hill, near Mfolozi, Zululand. Exact locality and age unknown. (Here refigured as Figs 17–20A.)



Fig. 17. *Paratexanites umkwelanense* (Crick, 1907). Holotype BMNH-C18134. Inner whorls of the specimen figured by Crick (1907, pl. 15 (fig. 9)).  $\times 1$ .



Fig. 18. *Paratexanites umkwelanense* (Crick, 1907). Holotype BMNH-C18134. Inner whorls of the specimen figured by Crick (1907, pl. 15 (fig. 9)).  $\times 1$ .

#### *Material*

SAS-36/3238-3239, Z975, NMB-D1060C, and PCZ-5694, locality 73, Mzinene River, Zululand, St Lucia Formation, Coniacian IV-V to possibly Santonian I; SAS-Z967, locality 91, Hluhluwe River floodplain, Zululand, St Lucia Formation, Coniacian IV or V; SAS-Z870 and SAS-H199/8, locality 83, Mason's Camp, False Bay; BMNH-C81505, locality 88, St Lucia Formation, Coniacian IV-V.





Fig. 19. *Paratexanites umkwelanense* (Crick, 1907). Holotype BMNH-C18134. Outer whorl of specimen figured by Crick (1907, pl. 15 (fig. 9)).  $\times 0,75$ .



Fig. 20. A. *Paratexanites umkwelanense* (Crick, 1907). Holotype BMNH-C18134, Outer whorl of specimen figured by Crick (1907, pl. 15 (fig. 9)).  $\times 0,75$ . B. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19449.  $\times 0,9$ .

*Dimensions*

|          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|------------|------------|----------------|------------|-------------|-------------|
| Holotype |          |            |            |                |            |             |             |
| C18134   | 125,0    | 52,0(41,6) | 50,0(45,2) | 0,96           | —          | 25          | 25          |
| 36/3238  | 63,0     | 24,0(38,1) | 24,0(38,1) | 1,0            | 22,0(34,9) | 17          | 17          |
| PCZ5694  | 112,0    | 41,0(36,6) | 43,0(38,4) | 0,95           | 44,0(39,3) | 19          | 19          |
| H199/8   | 140,0    | 44,0(31,4) | 50,0(35,7) | 0,88           | 59,0(42,1) | 25          | 25          |
| Z967     | 145,0    | 48,0(33,1) | 48,0(33,1) | 1,0            | 65,0(44,8) | 22          | 22          |
| Z870     | 185,0    | 53,0(28,6) | 65,0(35,1) | 0,82           | 74,0(44,3) | 11 × 2      | 11 × 2      |

*Description*

Coiling is evolute with an umbilical width of 35 to 45 per cent, increasing with diameter. Whorl overlap is very little and the dorsal zone of impression consequently extremely shallow. The whorl section is rounded subtriangular, with greatest costal and intercostal width at the umbilical tubercle, which is situated somewhat ventral of the umbilical edge (Figs. 21B-C).

Details of the early ontogeny are illustrated in SAS-36/3238 (Fig. 22) where the smooth stage continues up to a diameter of 5 mm. Following that, weak ribs with pinched, radially elongated umbilical tubercles appear, bifurcating occasionally. Ventrolateral tubercles become visible in the umbilical seam at a diameter of 20 mm. In this specimen ornament remains weak up to a

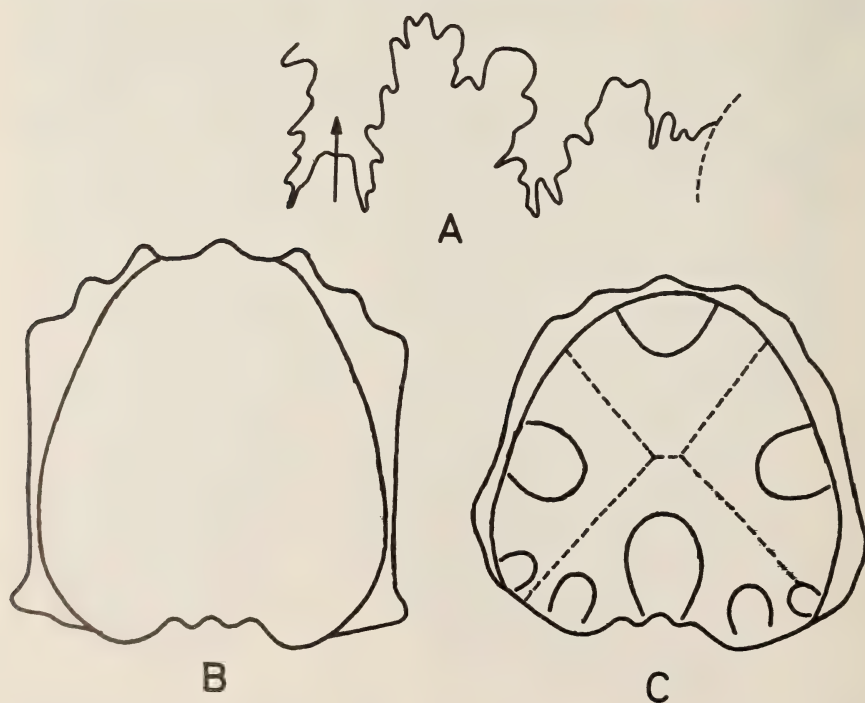


Fig. 21. *Paratexanites umkwelanense* (Crick, 1907). A. Partial suture of SAS-Z979. B-C. Whorl sections of SAS-36/3239 and SAS-Z967. All  $\times 1$ .





Fig. 22. *Paratexanites umkwelanense* (Crick, 1907). SAS-36/3238. Showing inner whorls to illustrate early ontogeny.

diameter of *c.* 30 mm. After this, ornament becomes very robust, with strong, single ribs connecting radially elongated umbilical tubercles, displaced somewhat up the flanks, to strong, spinose ventrolateral spines leaning against the umbilical wall or, in poorer preservation, prominent rounded nodes. Separation of the ventrolateral tubercle occurs in SAM-PCZ5694 (Fig. 23) at a diameter of 55 to 65 mm. At diameters of *c.* 100 mm the submarginal, marginal, and external rows of tubercles are equidistant. The keel is undulating in all the specimens. In some specimens the undulations are so prominent as to create the appearance of a central row of tubercles. In addition, low swellings may connect the external tubercles spirally and across the venter, producing a reticulate effect on the venter as in SAS-Z967 (Figs 24–26) and SAS-H199/8 (Fig. 27).

Ornament remains basically the same throughout the phragmocone. On the body chamber, which consists of at least two-thirds of a whorl, ornament becomes more prominent and acute, with distinct external tubercles protruding far beyond the height of the weakened, undulating keel (Figs 28–30).

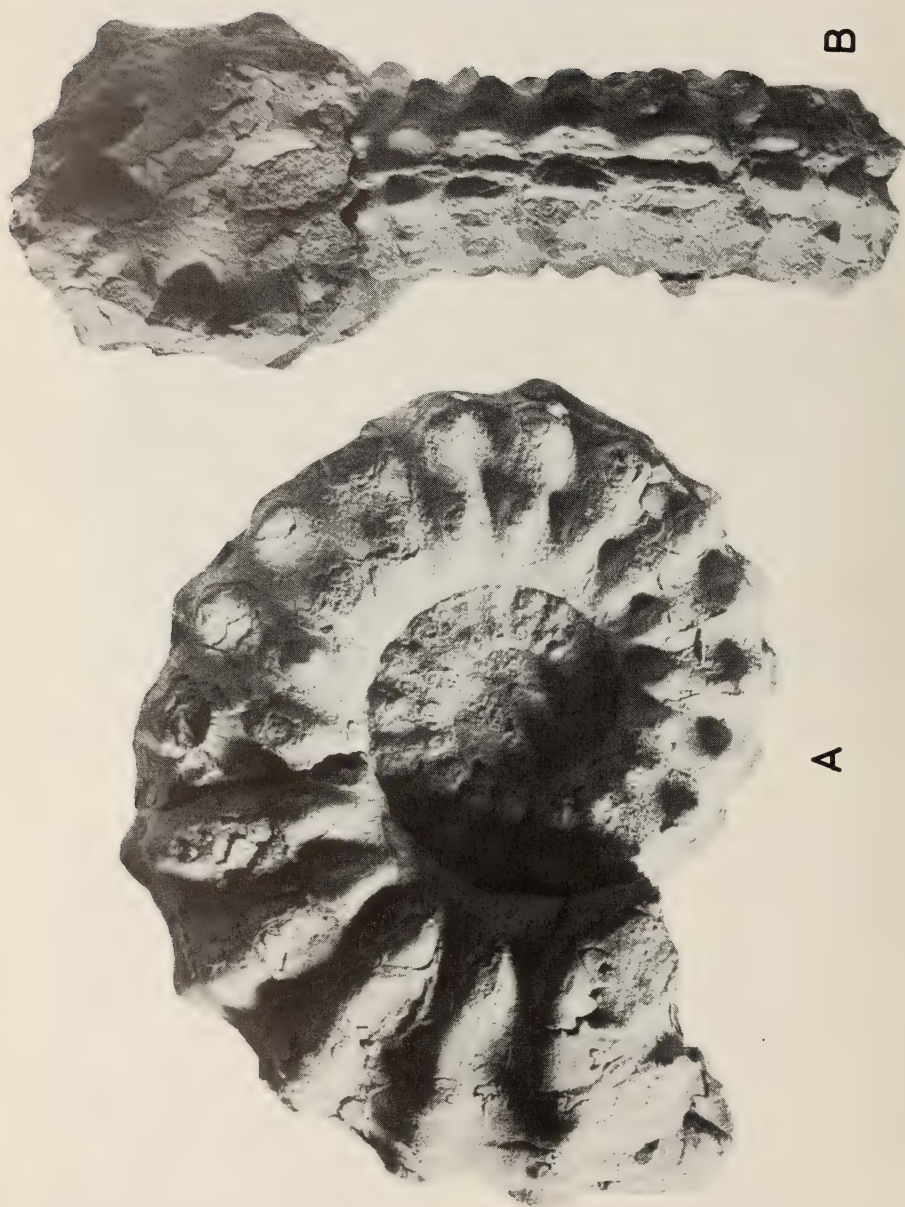


Fig. 23. *Paratexanites umkwelanense* (Crick, 1907). SAM-PCZ5694.  $\times 1$ .





Fig. 24. *Paratexanites umkwelanense* (Crick, 1907). SAS-Z967.  $\times 1$ .





Fig. 25. *Paratexanites umkwelanense* (Crick, 1907). SAS-Z967.  $\times 1$ .



Fig. 26. *Paratexanites umkwelanense* (Crick, 1907). SAS-Z967.  $\times 0,87$ .

### Discussion

This species was created *in passim* by Crick (1907: 228) by stating that 'with the collection from False Bay was also a specimen . . . from Umkwelane Hill referable to the genus *Mortoniceras* Meek. . . . Though related to the Pondoland forms *Mortoniceras soutoni* and *M. stangeri* it is specifically distinct therefrom and may be named *M. umkwelanense*.'



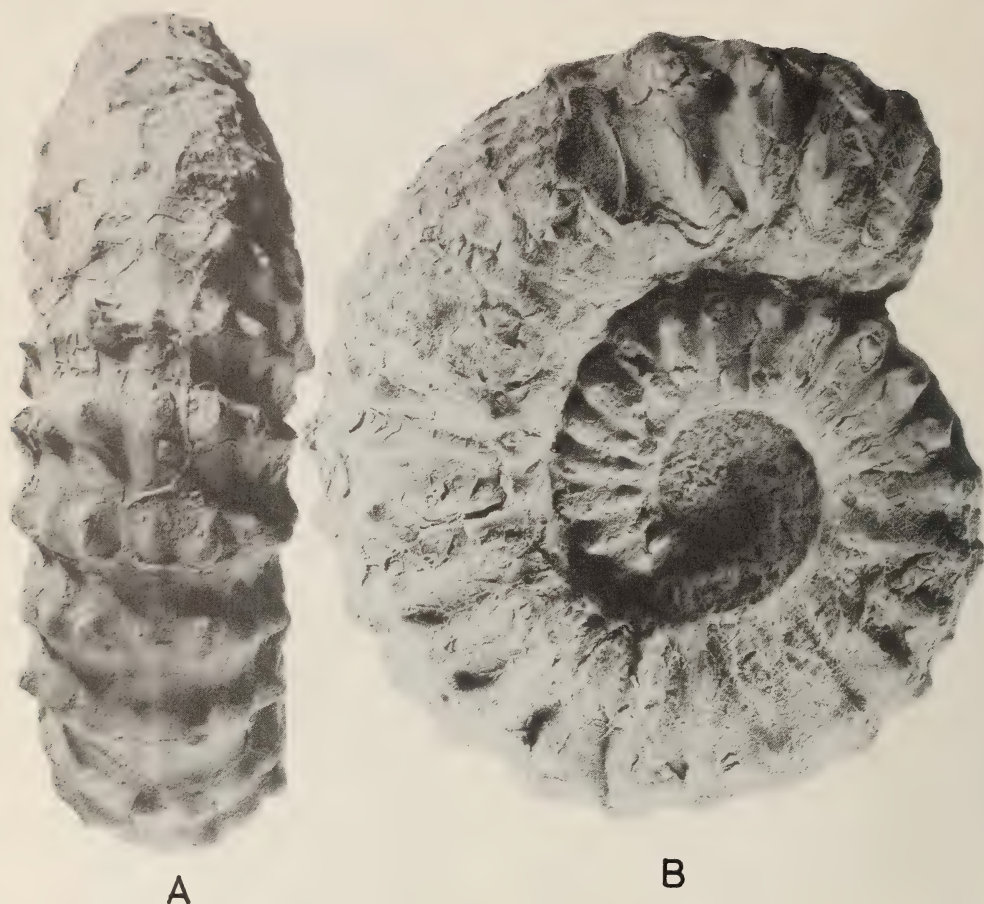


Fig. 27. *Paratexanites umkwelanense* (Crick, 1907). SAS-H199/8. Showing the undulating central keel.  $\times 0,64$ .

The inner and outer whorls of the holotype are here refigured photographically (Figs 17–20A) to illustrate the distinct ornament in the adult stage as well as the ontogeny.

In the adult, the species has very distinct ornament and is easily identified by the spinosity of the umbilical, submarginal and marginal tubercles, and the very clavate external tubercles protruding far above the undulating keel. The inner whorls are distinguished by the stout ornament and rounded, subtrigonal whorl section.

Matsumoto (1970: 255) pointed to the similarity between *P. umkwelanense* and *P. zeilleri* and suggested that, if sufficient material were available, distinction between the two species may prove to be of subspecific value only. *P. zeilleri* is difficult to interpret, being monotypic and having been figured once only, by De Grossouvre. According to De Grossouvre (1894: 67) the specimen figured





Fig. 28. *Paratexanites umkwelanense* (Crick, 1907). SAS-36/3239. Body chamber fragment illustrating generally spinose adult ornament.  $\times 1$ .



Fig. 29. *Paratexanites umkwelanense* (Crick, 1907). SAS-Z975. Atypical body chamber fragment lacking well-defined umbilical tubercles.  $\times 0,6$ .

by Schlüter (1876, pl. 6 (fig. 1a-b)) as *Ammonites texanus* belongs to *P. zeilleri*. Collignon (1948: 72) has, however, rather convincingly demonstrated that doubt exists as to the conspecificity of the two specimens. This thus leaves us with a single specimen on which to interpret *P. zeilleri*. *P. zeilleri* seems to differ mainly in having a slightly wider umbilicus (c. 47% according to De Grossouvre's figure) and lacking the prominent development of the umbilical tubercle.

Without having been able to examine De Grossouvre's original specimen, the authors are hesitant in referring the Zululand material to *P. zeilleri*, and prefer to refer it to *P. umkwelanense*.

The specimen referred to as *Mortoniceras* aff. *umkwelanense* by Spath (1921: 234, text-fig. D2) is definitely not a *Paratexanites*, but a good example of *Plesiotexanites* to be described below.



Fig. 30. *Paratexanites umkwelanense* (Crick, 1907). NMB-D1060. Body chamber fragment.  $\times 0,6$ .



*P. umkwelanense* is possibly derived from *Paratexanites australis* sp. nov. directly or via *P. orientalis* (Yabe), through becoming quadrituberculate at an earlier stage and in acquiring a more inflated whorl section. Similarities between *P. australis* and *P. umkwelanense* are striking, as far as the strong development of ornament in the relatively early stages of growth, the undulating keel, and faint reticulate pattern on the venter are concerned.

*P. orientalis* differs from *P. umkwelanense* mainly in having a more depressed whorl section in early stages of growth and less strongly developed ornament. The adult whorl section of *P. orientalis* (see Matsumoto 1970: 254, fig. 11(85)b), however, is very similar to that of *P. umkwelanense*, suggesting possible genetic relationships. In the latter respect the apparent lack of undulations on the keel of *P. orientalis* is disturbing.

*P. sellardsi* Young has also been compared with *P. zeilleri*, and Young (1963: 80) states that the 'differences between *Parabevahites zeilleri* and *P. sellardsi* are not beyond the realm of variation within a species'. *P. sellardsi*, however, is a distinct '*Parabevahites*' with an approximated submarginal and marginal tubercle. This latter characteristic is sufficient for separation of *P. sellardsi* and *P. umkwelanense*.

*P. rex* Matsumoto has similar coarse ornament, but has a compressed rectangular whorl section and lacks the spinose tuberculation of the adult of *P. umkwelanense*.

*P. muramotoi* Matsumoto, *P. compressus* Matsumoto, and *P. mikasaensis* Matsumoto, from Japan, can all be distinguished from *P. umkwelanense* on account of their more compressed whorl section.

Differences between *P. umkwelanense* and *P. pseudotricarinatum* sp. nov. are discussed below (p. 59).

### Occurrence

Upper Coniacian, Coniacian IV-V to possibly Lower Santonian, Santonian I of Zululand.

### *Paratexanites pseudotricarinatum* sp. nov.

Figs 31-44

### Holotype

SAS-Z813 (Figs 32-33), locality 91, near the Hluhluwe River estuary, Zululand, St Lucia Formation, Coniacian IV-V.

### Etymology

Refers to the pseudotricarinate ornament on the venter.

### Material

Paratypes are SAS-Z807, Z815b, Z818, Z975, and SAM-PCZ5693, all from the same locality as the holotype, St Lucia Formation, Coniacian IV-V;

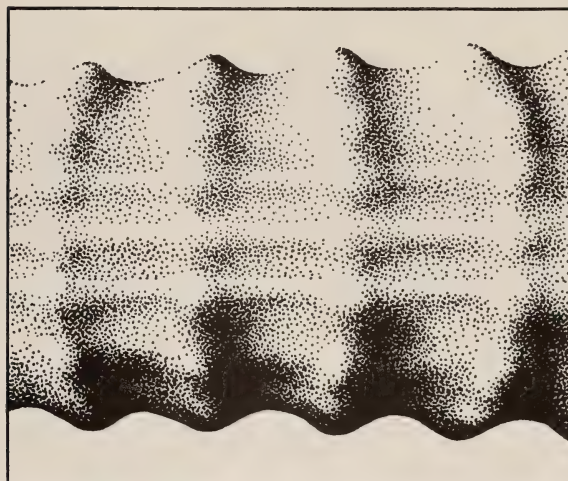


Fig. 31. *Paratexanites pseudotricarinatum* sp. nov. Drawing shows general ventral ornament of *P. pseudotricarinatum* composed of a series of rectangles formed by weak lateral keels and lateral ornament crossing over venter.

SAS-104, locality 89, boulder-strewn hill-slopes on the western boundary of the False Bay Game Park, St Lucia Formation, Coniacian IV; SAS-Z2110 and SAS-H198/1, locality 83, south-western shores of False Bay, Zululand, St Lucia Formation, Coniacian IV; NMB-D1060, locality 73, lower reaches of the Mzinene River, St Lucia Formation, Coniacian IV-V to possibly Santonian I; NMB-D1364 was reported from north of the Hluhluwe River Estuary, probably locality 86, St Lucia Formation, Coniacian IV; BMNH-C81505, between localities 91 and 92, St Lucia Formation, Coniacian IV-V.

#### Dimensions

|         | <i>D</i> | <i>Wb</i>  | <i>Wh</i>          | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|---------|----------|------------|--------------------|----------------|-------------|-------------|-------------|
| Z813    | 105,0    | —<br>53,0  | 38,0(36,2)<br>59,0 | —<br>0,89      | 30,0(37,1)  | 14 × 2      | 14 × 2      |
| D1060   | 202,0    | 56,0(27,7) | 65,0(32,2)         | 0,86           | 90,0(44,6)  | 21          | 21          |
| Z815    | 163,0    | 51,0(31,3) | 56,0(34,4)         | 0,91           | 77,0(47,2)  | 22          | 22          |
| PCZ5693 | 179,0    | 67,0(37,3) | 67,0(37,3)         | 1,0            | 102,0(56,8) | 22          | 22          |
| Z2110   | 205,0    | 70,0(34,1) | 67,0(32,7)         | 1,04           | 93,0(45,4)  | 25          | 25          |
| H198/1  | 187,0    | 61,0(32,6) | 61,0(32,6)         | 1,0            | 81,0(43,3)  | 27          | 27          |

#### Description

This is a very variable species but can be described as a *Paratexanites* in which the ribs sweep forward over the umbilical wall and flanks without, generally, forming a distinct umbilical tubercle. Ornament over the venter in the adult is striking (Fig. 31). Faint lateral keels connect the external (5) tubercles, whereas lateral ribbing continues weakened over the venter. The



Fig. 32. *Paratexanites pseudotricarinatum* sp. nov. Holotype SAS-Z813.  
Typical form.  $\times 0,8$ .





Fig. 33. *Paratexanites pseudotricarinatum* sp. nov. Holotype SAS-Z813. Ribbing here forms slight loops over venter. Typical form.  $\times 0,8$ .



Fig. 34. *Paratexanites pseudotricarinatum* sp. nov. Paratype SAS-104.  
Typical form.  $\times 0,8$ .



Fig. 35. *Paratexanites pseudotricarinatum* sp. nov. Paratype SAS-104. Typical form.  $\times 0,87$ .





Fig. 36. *Paratexanites pseudotricarinatum* sp. nov. Var. A Paratype SAS-Z807. Sparsely costate variety.  $\times 0,84$ .

central keel is broad and undulating. This thus gives rise to ornament on the venter comprising a series of rectangles.

### *Ontogeny*

The holotype (Figs 32–33) is the only specimen with part of the innermost whorls preserved. The smooth, rounded stage persists up to a diameter of 5 mm. Beyond that, ribs start appearing, bearing pinched, radially elongated umbilical tubercles. Rare bifurcations occur at this stage. The third row of tubercles



Fig. 37. *Paratexanites pseudotricarinatum* sp. nov. Var. B. Paratype NMB-D1060a. Compressed variety.  $\times 0,66$ .



Fig. 38. *Paratexanites pseudotricarinatum* sp. nov. Var. B. Paratype NMB-D1060a. Compressed variety.  $\times 0,76$ .





Fig. 39. *Paratexanites pseudotricarinatum* sp. nov. Var. C. Paratype SAS-Z2110.  
Variety with inflated whorls.  $\times 0,68$ .

appears in the umbilical seam only at a relatively late stage, *c.* 25 mm. Here these tubercles are flattened spinose, leaning against the umbilical wall. With increasing diameter the ventrolateral tubercles become less spinose, and move away from the umbilical seam, eventually to expose the fourth row of tubercles at a diameter of about 60 to 70 mm. Simultaneously, the whorl section becomes more rounded, lacking a distinct umbilical edge. Very faint indications of tuberculation become visible at midflank, foreshadowing the development of lateral



Fig. 40. *Paratexanites pseudotricarinatum* sp. nov. Var. C. Paratype SAS-Z2110. Variety with inflated whorls.  $\times 0,8$ .





Fig. 41. *Paratexanites pseudotricarinatum* sp. nov. Var. D. Paratype SAM-PCZ5693. Variety with wider umbilicus and stronger ventrolateral ornament.  $\times 0,57$ .

tuberculation in *Plesiotexanites*, but not distinct enough to merit reference to that subgenus. On the body chamber the whorl section becomes even more rounded, and the umbilical tubercle becomes virtually completely absorbed by the ribs.

#### *Variation*

Variation in the material is extreme, and mainly affects the density of ornament, strength of ornament over the venter, details of the whorl section and umbilical width. There are virtually as many varieties as specimens, and since the majority of specimens occur at more or less the same stratigraphic level, formal separations of these different morphotypes would lead to a profusion





Fig. 42. *Paratexanites pseudotricarinatum* sp. nov. Var. D. Paratype SAM-PCZ5693. Variety with wider umbilicus and stronger ventrolateral ornament. The ribs here pass strongly over the venter on the body chamber.  $\times 0,77$ .



Fig. 43. *Paratexanites pseudotricarinatum* sp. nov. Var. E. Paratype NMB-D1364. Variety with constrictions on body chamber resulting in serrate outline, and faint lateral tubercle on flanks, foreshadowing *Plesiotexanites* development.  $\times 0,6$ .

of meaningless names. In consequence, the most obvious varieties are here listed alphabetically with no formal taxonomic connotation.

Var. A, represented by SAS-Z807 (Fig. 36) differs from the typical form mainly in being much more coarsely costate throughout.

Var. B, represented by NMB-D1060a (Figs 37-38) and SAS-Z815 has a more compressed whorl section, with flattened flanks.

Var. C, represented by SAS-Z2110 (Figs 39-40) and SAS-H198/1 has a more inflated whorl section and high umbilical wall with clearly defined umbilical edge in the adult stage.

Var. D, is represented by one specimen only, SAM-PCZ5693 (Figs 41-42). Here ornament over the venter in the adult stage is strongest, with the ribs crossing the venter with little reduction of strength. Umbilical width in this specimen is also greatest at 56,8 per cent.

Var. E, represented by NMB-D1364 (Fig. 43) has slight constrictions towards the end of the phragmocone and on the body chamber, most noticeable on the venter, resulting in a serrate outline. In addition, the whorl section is most compressed in this specimen. Faint indications of a lateral tubercle are visible on the body chamber.

### Discussion

Unfortunately precise stratigraphic data are lacking, but it is to be expected that those specimens with faint indications of lateral tubercles would be youngest. *Plesiotexanites collignoniforme* sp. nov., described below, can be

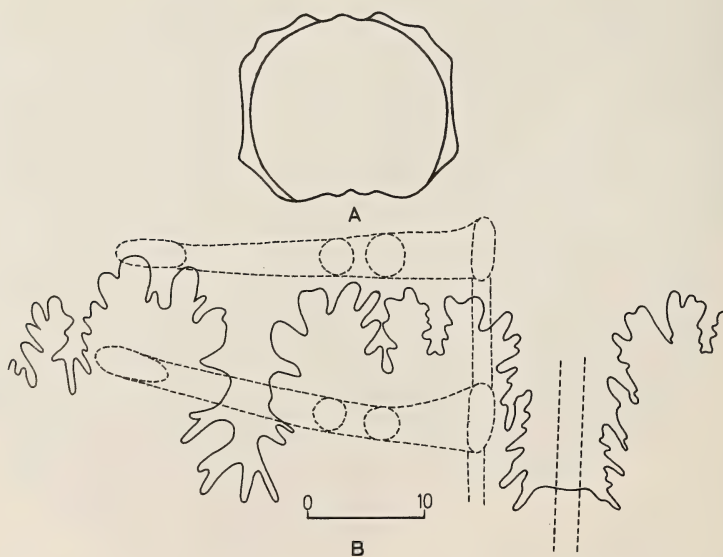


Fig. 44. *Paratexanites pseudotricarinatum* sp. nov. Paratype NMB-D1060. Whorl section and partial suture. Scale bar in millimetres.



derived from *Paratexanites pseudotricarinatum* through compression of the whorl section and addition of a lateral tubercle. The compressed specimen, NMB-D1364 (Fig. 43), here designated Var. E, is thus a potential intermediate form.

*Paratexanites umkwelanense* (Crick) is assumed to occur at more or less the same stratigraphic level, and the two species appear related. *P. umkwelanense* also has an undulating keel and may, in cases, also have indications of incipient lateral keels. In typical forms, however, adult ornament is much more spinose and conspicuous, and the ventral tubercles are elevated high above the keel.

*P. pseudotricarinatum* sp. nov. superficially resembles *P. zeilleri* as figured by De Grossouvre (1894, pl. 14 (fig. 1)), but is easily distinguished by the characteristic ventral ornament.

#### Occurrence

Coniacian IV–V, and possibly Santonian I of Zululand.

*Paratexanites* sp. aff. *P. serratomarginatus* (Redtenbacher, 1873)

Figs 45–47A

Compare:

*Ammonites serrato-marginatus* Redtenbacher, 1873: 110, pl. 25 (fig 2a–d).

*Paratexanites* (*Parabevahites*) *serratomarginatus* (Redtenbacher): Matsumoto, 1970: 260, pl. 36 (figs 1–3), text-fig. 16.

#### Material

SAS-Z633, Z814 and Z865, all from locality 91, near the Hluhluwe River Estuary, Zululand, St Lucia Formation, Coniacian IV–V.

#### Dimensions

|      | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|------|----------|------------|------------|----------------|------------|-------------|-------------|
| Z814 | 57,0     | 24,5(42,9) | 21,0(36,8) | 1,17           | 21,0(36,8) | 24          | 24          |
| Z865 | 70,0     | 28,0(40,0) | 28,0(40,0) | 1,00           | 25,0(35,7) | 27          | 27          |

#### Description

Coiling is relatively involute in the early stages, covering the ventral quarter of successive whorls, but becomes more evolute towards the body chamber. On the phragmocone the costal whorl section is subquadrate, as wide as high, or slightly wider than high with maximum width at the umbilical edge. In later whorls the section becomes more inflated, and subtrigonal (Fig. 45B) with no distinct umbilical edge.

Ornament, especially on the inner whorls of the three available specimens, differs considerably, ranging from dense, coarse ribbing with spinose ventro-lateral nodes as in SAS-Z814 (Fig. 47A) to dense ribbing lacking strong ventro-lateral ornament as in SAS-Z633 (Fig. 46). On the outer phragmocone whorls, ornament is similar in the three specimens, consisting of strong, radially elongated umbilical tubercles connected by weak, slightly prorsiradiately curved

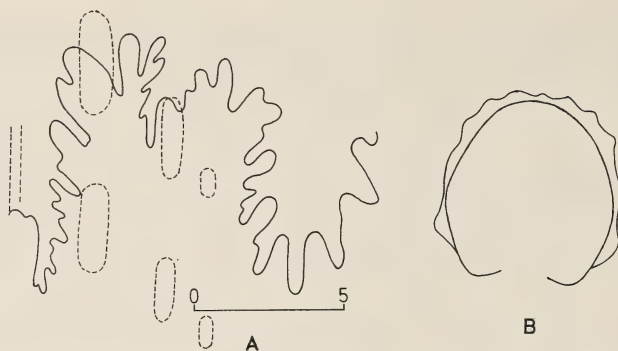


Fig. 45. *Paratexanites* sp. aff. *P. serratomarginatus* (Redtenbacher, 1873). SAS-Z814. Whorl section and partial suture. Scale bar in millimetres.

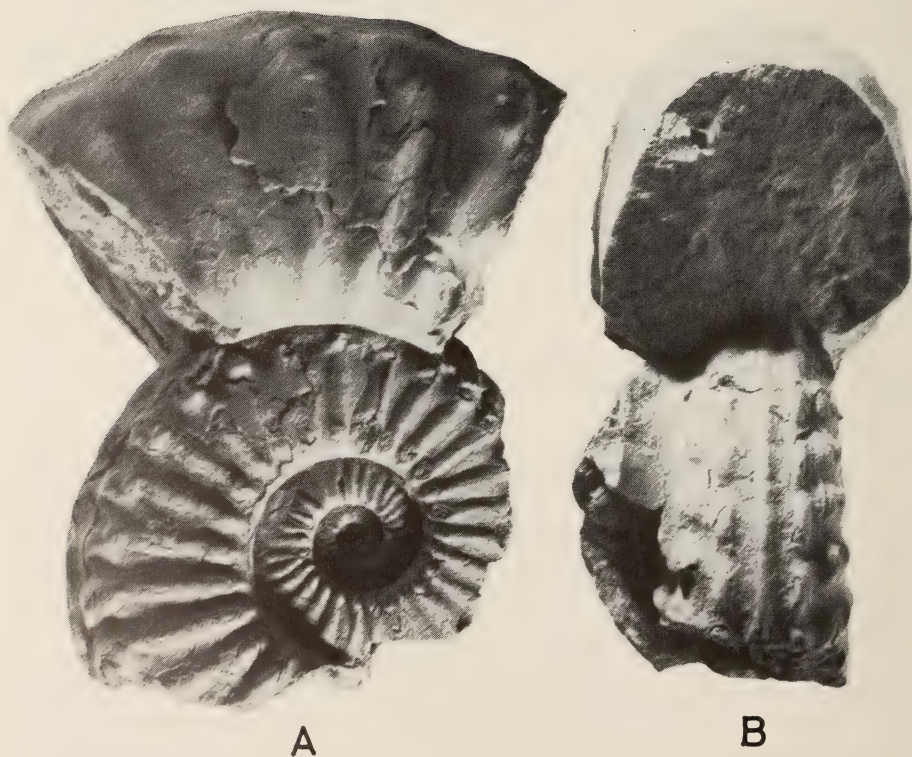


Fig. 46. *Paratexanites* sp. aff. *P. serratomarginatus* (Redtenbacher, 1873). SAS-Z633. Specimen with densely costate inner whorls.  $\times 1$ .

ribs to approximated submarginal and marginal tubercles and a slightly more distant row of clavate external tubercles.

The keel in all three specimens is undulating, though least noticeable in SAS-Z814, the specimen with strong ornament on the inner whorls. Parts of the body chamber are preserved in the two specimens, and here submarginal (3), marginal (4), and external (5) tubercles are virtually equidistant.

The external suture is partly exposed in SAS-Z814 (Fig. 45A).

### Discussion

It is unfortunate that the authors' material of the species is limited, as it would have been interesting to see whether there are any significant differences between those specimens with coarse early ornament and those with more delicate ornament. For the present all the specimens are referred to one species.

As far as the involute coiling and general nature of ornament on the outer phragmocone whorls are concerned, there is strong resemblance to *Paratexanites serratomarginatus*; especially when comparing SAS-Z814 (Fig. 47A) to Redtenbacher's figure (1873, pl. 25 fig. 2c-d).

This species, however, presents difficulties in interpretation. Of the seven specimens available to Redtenbacher, only two were figured. Subsequent interpretations of this species have differed considerably. Matsumoto (1970: 262 ff.) provided a good discussion on the extent and affinities of the species, and erected a new subspecies, *P. serratomarginatus grossouvrei*, to accommodate the French Villedieu specimens with undulating keels and stronger submarginal tubercles. The Zululand material resembles the French subspecies closest in possession of the undulating keel, but does not retain the double row of tubercles to such a large diameter.

None of the figured specimens of *P. serratomarginatus* shows satisfactorily whether the submarginal and marginal tubercles remain approximated throughout or whether this feature is restricted only to the phragmocone. This is the main reason for not accepting the subgeneric term *Parabevahites*, of which *P. serratomarginatus* is the type species. Until this question is resolved, it is advisable to refer to the Zululand material as *P. sp. aff. P. serratomarginatus*.

Not having seen the specimen, the authors cannot comment on the identity of the large fragment (referred to *P. serratomarginatus*) mentioned by Collignon (1948: 84), apart from the fact that the locality data appear to be incorrect. Collignon suspected the specimen to have come from the vicinity of Skoenberg, but it is more likely to have been collected in the lower reaches of the Mzinene River (Kennedy & Klinger 1975, locality 73) where *Paratexanites* species are known to occur. As yet *Paratexanites* species have not been recorded from the Skoenberg itself by the authors, and this seems unlikely to happen, as the youngest strata exposed there are Lower Coniacian.

This species is allied to *P. umkwelanense*, differing mainly in being more narrowly umbilicate and having more inflated whorls and denser, though not as prominently developed, ornament.



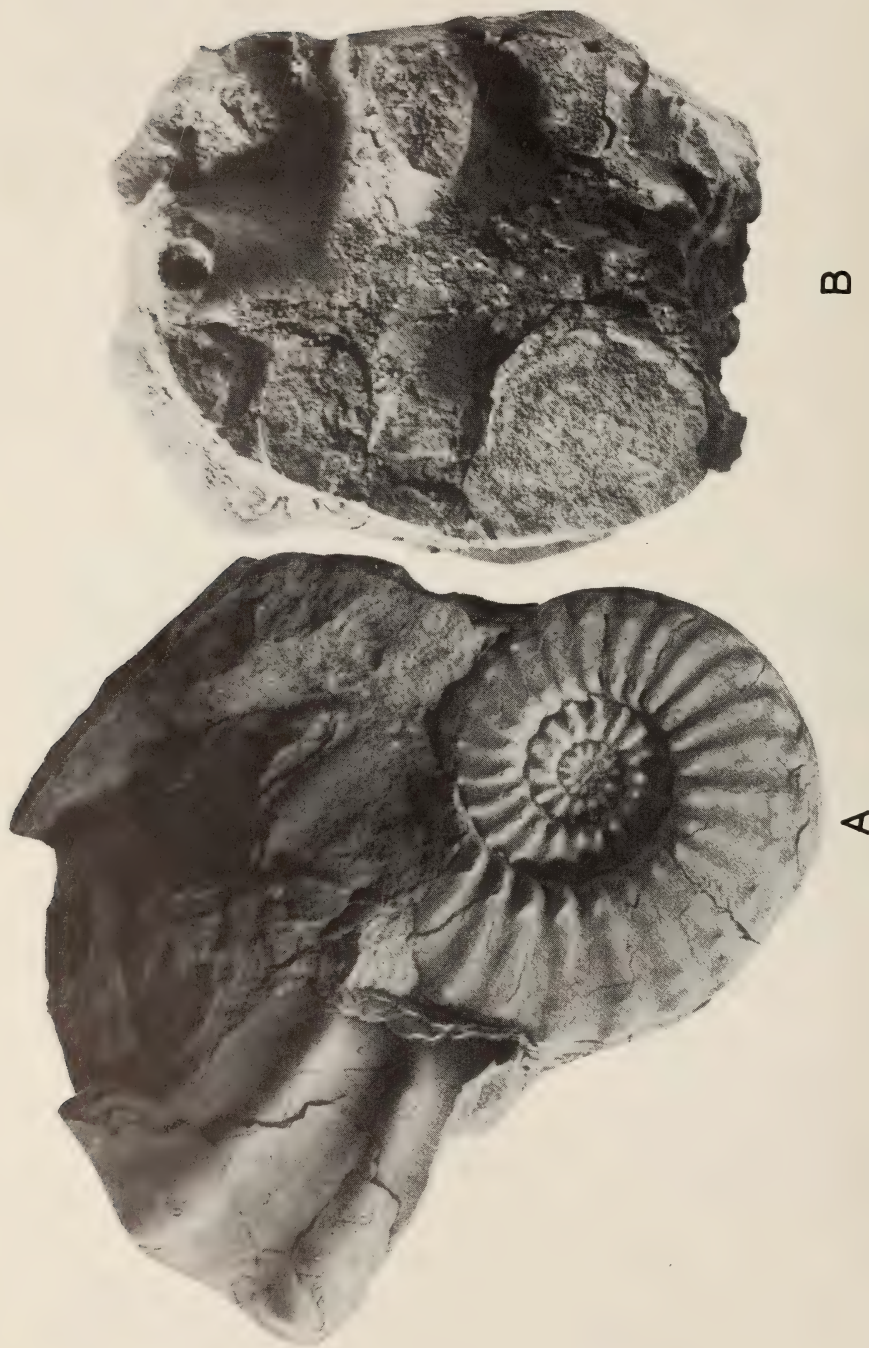


Fig. 47. A. *Paratexanites* sp. aff. *P. serratomarginatus* (Redtenbacher, 1873). SAS-Z814. Specimen with coarse inner whorls. B. *Paratexanites* sp. aff. *P. enscheris* (Schlüter, 1876). SAS-H1A/3. Whorl section. Note the large siphuncle.  $\times 1$ .

*Occurrence*

Coniacian IV–V of Zululand.

*Paratexanites* sp. aff. *P. emscheris* (Schlüter, 1876)

Figs 47B–48

*Compare:*

*Ammonites emscheris* Schlüter, 1876: 155, pl. 42 (figs 8–10).

*Material*

SAS–H1A/3, locality 22, Nyalazi River, Zululand, St Lucia Formation, Coniacian IV.

*Description and discussion*

A large septate fragment collected from the basal beds exposed at locality 22 (Klinger & Kennedy 1975) is tentatively referred to Schlüter's (1876) species. The costal whorl section is subrectangular, higher than wide with well-developed submarginal, marginal and external tubercles. The umbilical tubercles are radially elongated, thus differing from Schlüter's illustration (1876, pl. 42 (figs 8–10)).

Matsumoto (1970) recently discussed the scope of this species, pointing out that it is not well defined. One of the specimens included under the name *Ammonites emscheris* by Schlüter (1876: 155), previously described by him (1872: 42 pars., pl. 12 (figs 1–3)) as *Ammonites texanus*, was regarded by Matsumoto as being sufficiently different from *P. emscheris* to merit separate specific rank as *Paratexanites rex*. In the present specimen the umbilical tubercles are radially elongated as in the latter species, but the whorl section is not as compressed.

For the present it is considered best to refer to the available specimen as *P. sp. aff. P. emscheris*.

*Occurrence*

Coniacian IV of Zululand.

Genus *Plesiotexanites* Matsumoto, 1970

*Type species*

*Mortoniceras kawasaki* Kawada, 1929, by the original designation of Matsumoto (1970: 267).

*Diagnosis*

The inner whorls remain trituberculate (1,3+4,5) for a considerable period. Eventually the ventrolateral (3+4) node, which may be very large, divides into two distinct tubercles, submarginal (3) and marginal (4). Simultaneously, or later, a lateral (2) tubercle appears. Tubercles (3) and (4) may remain close together, or separate completely, giving rise to normal *Texanites* ornament.

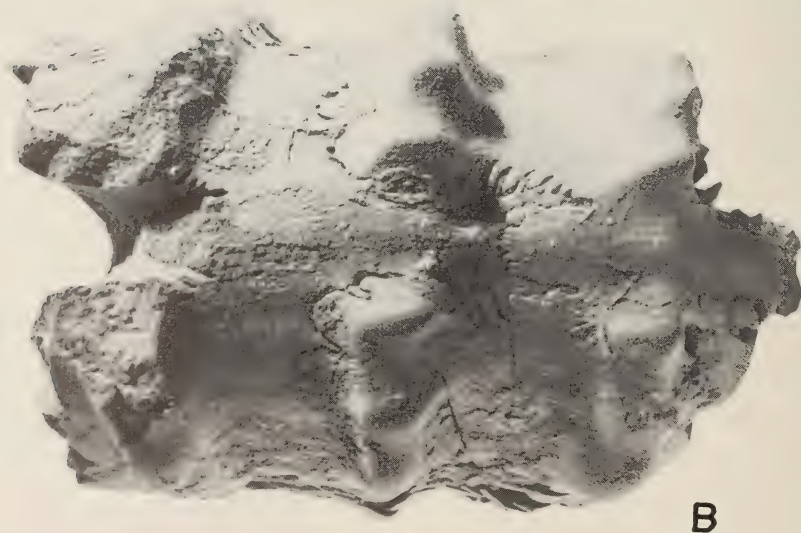


Fig. 48. *Paratexanites* sp. aff. *P. emscheris* (Schlüter, 1876). SAS-H1A/3.  $\times 1$ .



The lateral (2) tubercle may become prominent, remain inconspicuous, or become absorbed in the flanks in later stages of growth.

### Discussion

Matsumoto (1970: 274–280), in erecting *Plesiotexanites* as a subgenus of *Texanites*, discussed its affinities extensively, and, apart from some new data and comments on the phylogeny, it requires little elaboration.

According to Matsumoto (1970: 274–280) the following species were considered to be representatives of *Plesiotexanites*:

- Plesiotexanites kawasaki* (Kawada, 1929) (Matsumoto 1970: 280, pl. 38 (figs 1–2), pl. 39 (fig. 1), pl. 40 (figs 1–2), pl. 41 (fig. 1), pl. 42 (fig. 4), pl. 43 (figs 1–2), text-figs 21–22) from the Middle Santonian of Hokkaido.
- Plesiotexanites pacificus* Matsumoto (1970: 289, pl. 42 (fig. 2), pl. 45 (figs 1–2), pl. 46 (fig. 4), text-fig. 24) from the Santonian of Hokkaido.
- Plesiotexanites sanushibense* (Yabe & Shimizu) (1925: 132, pl. 33 (figs 3–5)) from the Santonian of Hokkaido.
- Plesiotexanites schlueteri* Matsumoto (1970: 278, text-fig. 20) from an unspecified horizon in northern Germany.
- Plesiotexanites shiloensis* (Young) (1963: 89, pl. 46 (figs 1–4), pl. 54 (figs 4–7), pl. 70 (figs 5–6, 8) text-fig. 24d) from the Upper Santonian of the Gulf Coast of North America.
- Plesiotexanites stangeri* (Baily) (1855: 455, pl. 11 (fig. 2)) from the Lower to Upper Santonian of South Africa, Madagascar, Hokkaido, and the Gulf Coast of North America.
- Plesiotexanites candelariae* (Young) (1963: 102, pl. 56 (figs 1, 3–4), pl. 60 (fig. 8), text-figs 20b, 28af, 29ae, 34af) from the Lower Campanian of the Gulf Coast of North America.
- Plesiotexanites thomsoni* (Jones) (1966: 200, pl. 26 (figs 1–8), text-fig. 2) from the Upper Coniacian or Santonian of California.
- Plesiotexanites transitorius* (Collignon) (1966a: 80, pl. 488 (fig. 1970A–B)) from the Middle Santonian of Madagascar.
- Plesiotexanites yezoensis* Matsumoto (1970: 294, pl. 44 (fig. 2)) from the Santonian of Hokkaido.

Some doubtful contenders mentioned by Matsumoto were:

- Texanites angolanus* Haas (1942: 12, figs 8–10, pl. 15 (fig. 11)) from the Santonian of Angola.
- Parabevahites dubius* Collignon (1966a: 133, pl. 513 (fig. 2026)) from the Upper Santonian of Madagascar.
- Mortoniceras omeraense* Reeside (1927: 38, pl. 42 (figs 3–4), pl. 43 (figs 1–2)) from the Santonian of New Mexico.
- Submortoniceras* (?) aff. *soutoni* Reyment (1955: 95, pl. 33 (fig. 1a–b)) from the Santonian of Nigeria.

To the list of definite representatives of *Plesiotexanites* may be added:

*Plesiotexanites matsumotoi* sp. nov.

*Plesiotexanites collignoniforme* sp. nov.

from the Santonian of Zululand and Pondoland.

*Plesiotexanites* sp. indet. from the Santonian of Zululand, a doubtful contender.

The diagnostic characteristics of *Plesiotexanites* are restricted to the ontogenetic development of ornament. Clearly this presents difficulties when dealing with incomplete material, as Matsumoto (1970: 276) indicated in discussing the affinities of *Texanites angolanus* and *T. ralijaonai*, both of which lack the inner whorls. This should, however, in no way prevent the use of the name *Plesiotexanites* for a group of generally evolute texanitids occupying an intermediate position between *Paratexanites* or *Protexanites* and *Texanites*, and which also probably gave rise to *Reginaites*.

The ontogeny of *Plesiotexanites* provides clues to its origin. The initial trituberculate stage is like that of *Protexanites* s.s. The succeeding stages of the various species differ in respect of the stage of appearance of the lateral tubercle and division of the ventrolateral node. Thus, in *P. stangeri* the ventrolateral node divides before the development of the lateral tubercle, thus mimicking a *Paratexanites* type of ornament. With the development of the lateral tubercle, the ornament is like that of *Texanites* s.s. In *P. schlueteri* the lateral tubercle is retained for a short period only, thus the *Texanites* ornament here gives way to *Paratexanites* ornament in the adult stage. In species such as *P. thomsoni* and *P. matsumotoi* sp. nov. the lateral tubercle appears before division of the ventrolateral node, thus producing *Protexanites* (*Anatexanites*)-like ornament. According to Matsumoto (1970: 277), *Texanites shiloensis* Young, which should also be referred to *Plesiotexanites*, has inner whorls allied to *Protexanites* (*Miotexanites*) *minimus* Matsumoto.

*P. matsumotoi* sp. nov. has inner whorls comparable to those of *Paratexanites australis* sp. nov., and *P. collignoniforme* sp. nov. has inner whorls similar to those of *Paratexanites pseudotricarinatum* sp. nov. or *P. umkwelanense* (Crick).

Available data thus would seem to suggest that the origin of *Plesiotexanites* is to be found in *Protexanites* s.l. or in *Paratexanites*.

The South African material of *Plesiotexanites* is of extreme interest in providing links to both *Reginaites* and *Texanites* s.s., and is here accorded full generic rank.

#### *Occurrence*

Definite occurrences of *Plesiotexanites* are in the Santonian of Japan, Germany, Gulf Coast of America, Madagascar, Zululand, and Pondoland. Other possible occurrences are in the Santonian of Angola, Cameroons and Western Interior of North America.

*Plesiotexanites stangeri* (Baily, 1855)

Figs 20B, 49–69

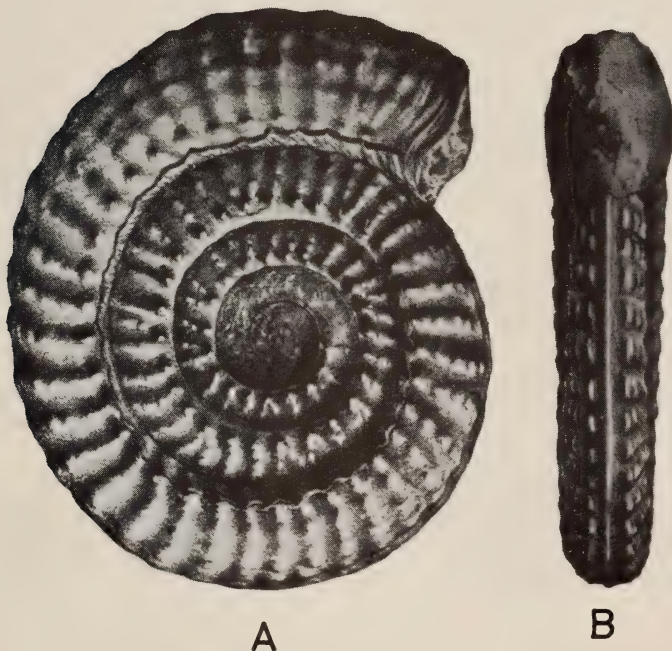
*Ammonites stangeri* Baily, 1855: 455, p. 11 (fig. 2).*Mortoniceras stangeri* (Baily): Woods, 1906: 338, pl. 44 (fig. 1). Spath, 1921: 297, text-fig. D-1; 1922: 137, pl. 9 (fig. 2).*Mortoniceras stangeri* (Baily) var. *densicosta* Spath, 1922: 138, pl. 5 (fig. 2).*Mortoniceras stangeri* (Baily) var. *sparsicosta* Spath, 1922: 138, pl. 5 (fig. 1).*Texanites stangeri* (Baily): Young, 1963: 88, pl. 45 (figs 1–3), text-fig. 25p.*Texanites stangeri* (Baily) *densicostus* (Spath): Young, 1963: 86, pl. 42 (figs 3–4), pl. 43 (figs 2–4), pl. 47 (figs 5–6), pl. 48 (figs 2, 5–6), pl. 71 (figs 1–4), text-figs 25c, e, g–h, 34c.*Texanites stangeri* (Baily) var. *densicosta* (Spath): Collignon, 1966a: 72, pl. 484 (fig. 1958), pl. 512 (fig. 2024).*Texanites stangeri* (Baily) var. *sparsicosta* (Spath): Collignon, 1966a: 62 pl. 479 (fig. 1951).*?Parabevahites* cf. *emscheri* Collignon, 1966a: 80, pl. 488 (fig. 1966).*Texanites stangeri* subsp. aff. *densicostus* (Spath): Wolleben 1967: 1152, pl. 149 (fig. 1).*Texanites* (*Plesiotexanites*) *stangeri* (Baily): Matsumoto, 1970: 285, pl. 41(45) (figs 2–4), text-fig. 23 (97). Kennedy & Klinger, 1973: 102.*Texanites* (*Plesiotexanites*) *stangeri* (Baily) *sparsicosta* (Spath): Kennedy & Klinger, 1973: 102, pl. 6 (fig 3a–b).*Texanites* (*Plesiotexanites*) *stangeri* (Baily) *densicosta* (Spath): Kennedy & Klinger, 1973: 102, pl. 5 (fig. 2a–b).*Texanites* (*Plesiotexanites*) *stangeri* (Baily) var. indet. Kennedy & Klinger, 1973: 103.

Fig. 49. *Plesiotexanites stangeri* (Baily, 1855). Copy of Baily's original figure (1855, pl. 11 (fig. 2)). Baily's figure is a mirror image and partially restored. See Figs 50 and 51.)





Fig. 50. *Plesiotexanites stangeri* (Baily, 1855). Cast of holotype BMNH-C-73333.  $\times 0,42$ .

#### *Type*

Holotype is BMNH-C73333, the specimen figured by Baily (1855, pl. 11 (fig. 2)) (Fig. 49) from the Umzamba Estuary, Transkei, Umzamba Formation, here refigured as Figures 50–51.

#### *Material*

BMNH-C19443, C19446, C19449–C19450, C19455–C19457, C19462, C35623, C35627, C53144, SAM-K4827, K5544–K5545, K5547–K5551, NMB-D1604, all from locality 1, from the Umzamba Formation at Umzamba



Fig. 51. *Plesiotexanites stangeri* (Baily, 1855). Cast of holotype BMNH-C-73333.  $\times 0,48$ .

Estuary, Transkei, Santonian II–III; DM–3505, UN–6557, UN–6564, UN–6570; localities 4 and 5, subsurface deposits at Durban, Umzamba Formation, Santonian III to Campanian I; several unmarked specimens in the Geological Survey Collection, Pretoria, from excavations at locality 6, the Enseleni Game Reserve, St Lucia Formation, Santonian II to Campanian I; similar fragments from locality 14 in road cuttings near Mfolozi, St Lucia Formation, Santonian II to Campanian I; a single fragment SAS–Z1971, locality 74, north-western part of False Bay at Die Rooiwal, St Lucia Formation, Santonian I–Campanian I; and BMNH–C81533, locality 81, St Lucia Formation, Santonian I–II.

### Dimensions

|           | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|-----------|----------|------------|------------|----------------|-------------|-------------|-------------|
| C73333    | 320,0    | 60,8(19,0) | 83,0(26,0) | 0,73           | 179,2(56,0) | 39          | 39          |
| C19443    | 120,5    | —          | 32,0(26,0) | —              | 49,0(41,0)  | 24          | 24          |
|           | 64,0     | —          | 16,6(26,0) | —              | 30,6(47,9)  | 19          | 19          |
|           | 32,0     | —          | 9,3(29,1)  | —              | 14,6(45,8)  | 17          | 19          |
| C19446    | 135,0    | —          | 39,0(28,8) | —              | 69,0(50,3)  | 28          | 28          |
|           | 70,0     | —          | 22,0(31,4) | —              | 34,0(48,5)  | 20          | 26          |
|           | 34,0     | 10,0(29,4) | —          | —              | 9,4(27,6)   | 19          | 27          |
| C19449    | 211,0    | 46,6(22,0) | 55,7(26,4) | 0,83           | 112,8(53,4) | 30          | 30          |
|           | 112,8    | —          | 34,2(30,4) | —              | 40,0(57,1)  | 23          | 27          |
| C19450    | 138,6    | —          | 34,6(25,0) | —              | 74,6(53,8)  | —           | —           |
|           | 74,6     | —          | 22,6(30,3) | —              | 37,3(50,0)  | 18          | 32          |
| C19455    | 137,0    | 36,0(26,2) | 27,7(20,2) | 1,29           | 67,0(48,9)  | 23          | 29          |
|           | 67,0     | —          | 24,0(35,8) | —              | 33,0(49,2)  | 19          | 27          |
| SAM–K5547 | 139,0    | 39,0(28,0) | 41,0(29,4) | 0,95           | 72,0(51,7)  | 23          | 29          |
|           | 72,0     | 25,0(34,0) | 22,0(30,5) | 1,1            | 38,0(52,7)  | 14          | 30          |
| SAM–K5550 | 54,0     | 16,6(29,6) | 15,0(27,7) | 1,06           | 24,0(44,4)  | 19          | 21          |

### Description

Coiling is very evolute, polygyral, with an average umbilical width of the order of 40 to 50 per cent of the total diameter, but may reach up to 60 per cent in some specimens. The whorl overlap is very little; generally less than 10 per cent of the total whorl height. The species may grow up to a very large size; the holotype is the largest known specimen with a diameter of 320 mm. The majority of the Umzamba specimens measure between 100 to 200 mm.

Increase in whorl section is rapid. The innermost whorls have a square to depressed whorl section, but, with increase in diameter, the section becomes more rounded and gradually higher than wide with a rounded umbilical wall and venter (Fig. 52A–B).

Ornament is variable due to ontogenetic change and intraspecific variation.

### Ontogeny

In the first, *Protexanites* stage, which lasts up to *c.* 40 mm (Fig. 53B–C), ornament is trituberculate, consisting of small, conical umbilical (1) tubercles, and much larger, clavate ventrolateral (3+4) nodes, situated in the umbilical suture and leaning against the umbilical wall of the succeeding whorl. The external (5) tubercles are situated on either side of a prominent central keel,



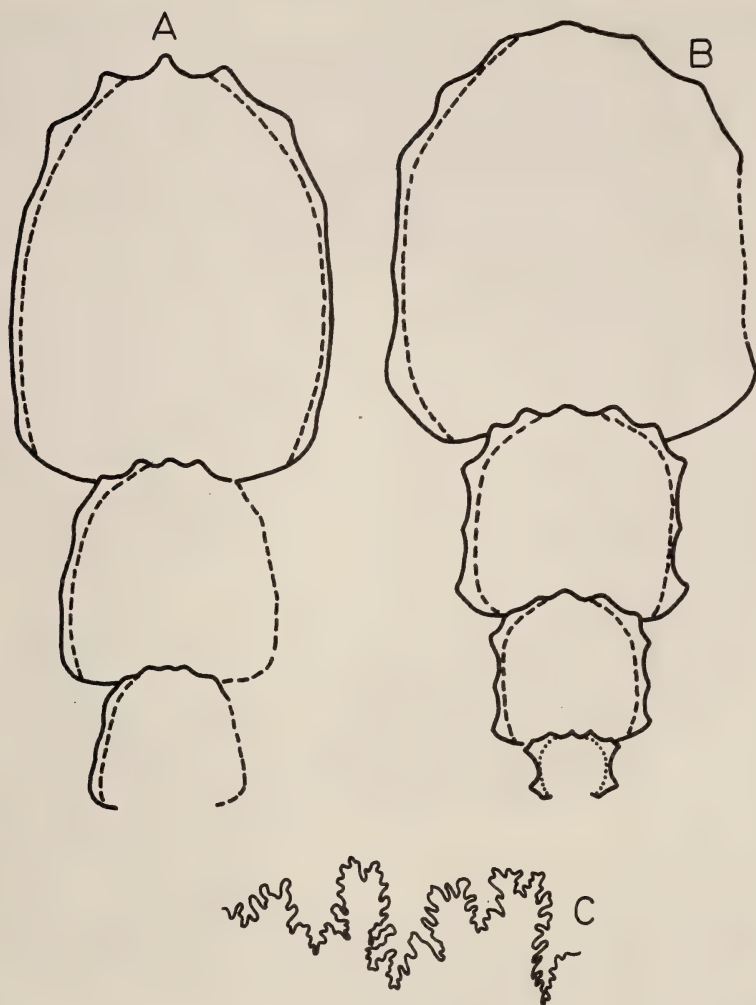


Fig. 52. *Plesiotexanites stangeri* (Baily, 1855). A. Whorl section of holotype BMNH-C73333, after Matsumoto (1970, text-fig. 23(97)A). B. Whorl section of var. *sparsicosta*, BMNH-C73333, after Matsumoto (1970, text-fig. 23(97)B). C. Partial suture of BMNH-C19444, after Spath (1921, fig. D-1a).

which is already developed at a diameter of 7,5 mm. These tubercles are joined to the bases of the large ventrolateral nodes by low, broad connections. They are not aligned with the ventrolateral (3+4) and umbilical (1) tubercles, but are displaced somewhat forward. The external tubercles are very variable, sometimes being elongated spirally to such an extent as to form discontinuous lateral keels (Fig. 54E-F).

In the second stage, the ventrolateral tubercles begin to separate into two

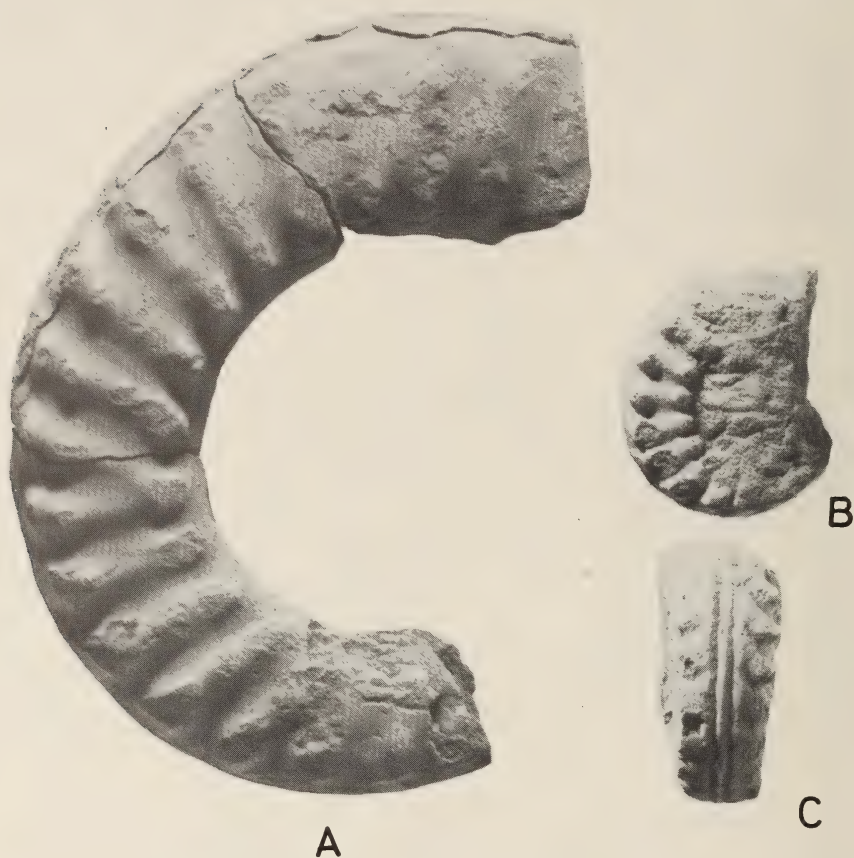


Fig. 53. *Plesiotexanites stangeri* (Baily, 1855). A. SAS-Z1971. One of the two specimens of the species thus far found in the False Bay region of Zululand. B-C. SAM-K5889. Juvenile specimen showing pseudotricarinate inner whorls.  $\times 1$ .

different rows through the splitting off on the ventral side of a new row, though still connected by a common base (Fig. 54A-C). This is the '*Parabevahites*' stage. With increasing diameter the inner of these two rows migrates dorsad from the spiral suture to complete the separation of the two rows. This is the '*Paratexanites*' stage.

In the third stage of development, faint indications of the lateral (2) tubercle start appearing near the dorsal third of the flanks. The moment of appearance and the strength of these lateral tubercles are very variable.

On the later part of the phragmocone, and on the body chamber, which consists of one whorl on the holotype (Figs 50-51), bifurcations cease and ribbing becomes single. The whorl section becomes progressively inflated and towards the last part of the body chamber all lateral ornament weakens.

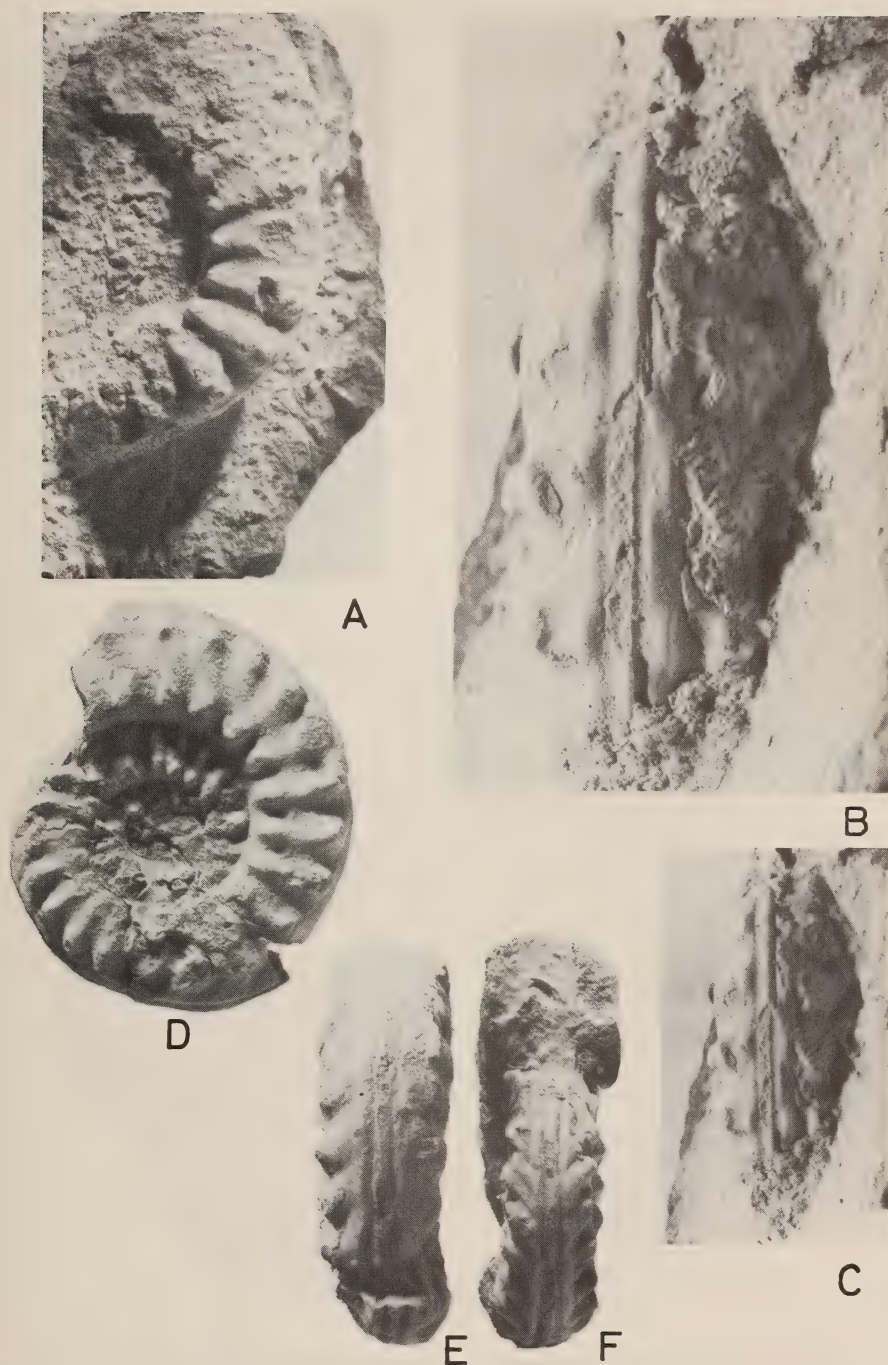


Fig. 54. *Plesiotexanites stangeri* (Baily, 1855). A-C. SAM-PCZ5686. Specimen illustrating the *Paratexanites* stage of ontogeny, but with distinct separated external tubercles. D-F. SAM-K5550. Similar specimen with wavy lateral pseudo-keels. A, C, D-E  $\times 1$ ; B  $\times 2$ .



*Intraspecific variation*

Variation in density and prominence of ornament is extensive in this species, and has led to the usage of names such as '*sparsicosta*' and '*densicosta*', initially adopted by Spath (1922: 138). These varietal names are applicable mainly to density of ribbing on the inner whorls as shown by Spath (1922, pl. 5 (figs 1-2)) and here as Figures 57, 58. The present material shows that virtually all transitions occur from closely ribbed specimens, SAM-K5447 (Fig. 59), BMNH-C19443 (Fig. 60), via the holotype of the typical form (Figs 50-51) to the holotype of var. '*densicosta*' (Figs 55-57). Apart from density, differences exist in strength of ornament on later parts of the shell.



Fig. 55. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19456. Holotype of var. *densicosta*. (British Museum photograph.)  $\times 1$ .

Specimens such as BMNH-C19462 (Figs 61-62A) and BMNH-C19449 (Figs 62B, 63) still have strongly developed ribbing and tuberculation on the outer whorls, whereas specimen BMNH-C19459 (Figs 64-65) or BMNH-C19456 (Figs 55-56), the holotype of var. '*densicosta*', are virtually devoid of ornament at the same diameters. Density of ribbing on the inner whorls of the latter two specimens clearly shows that strength of ribbing on the outer whorls is independent of density of ribbing on the inner whorls.

The point of appearance of the lateral (2) tubercle is extremely variable,



Fig. 56. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19456. Holotype of var. *densicosta*. (British Museum photograph.)  $\times 1$ .



Fig. 57. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19456. Close-up of inner whorls of var. *densicosta*.  $\times$  c. 3.



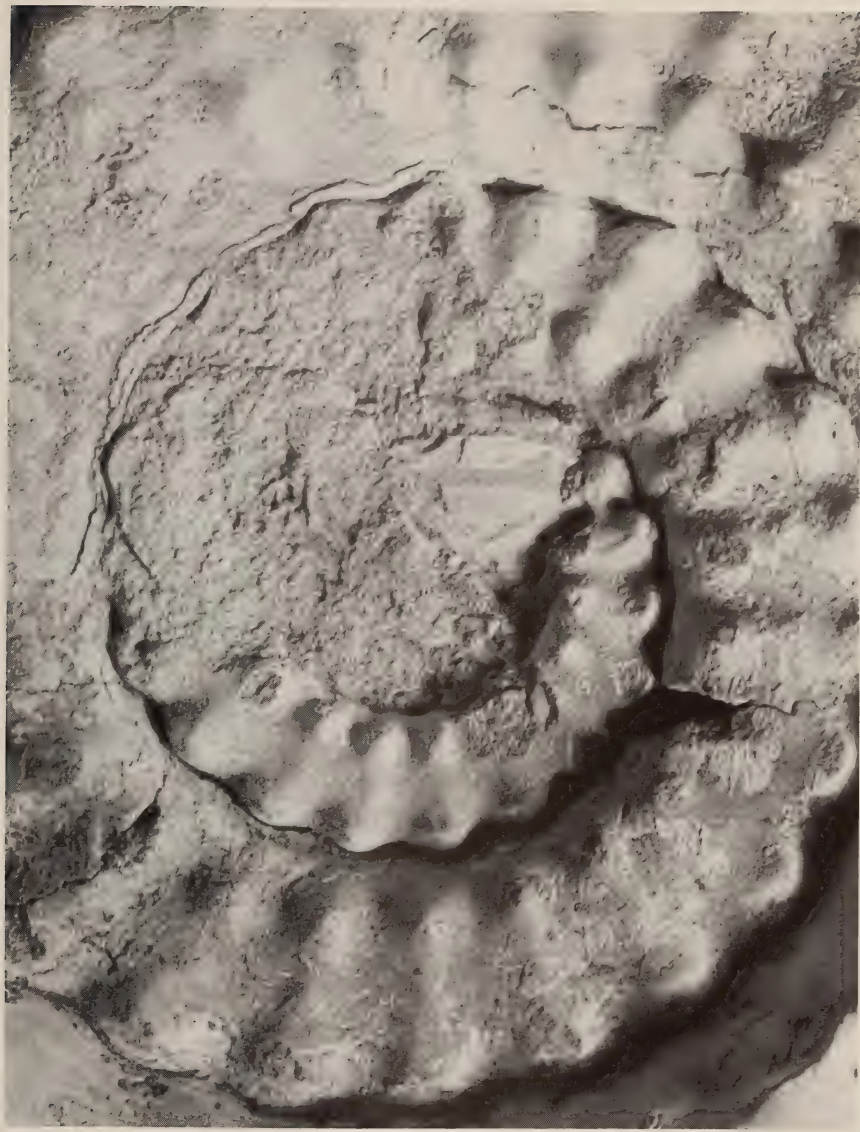


Fig. 58. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19444. Close-up of inner whorls of var. *sparsicosta*.  $\times c. 3$ .

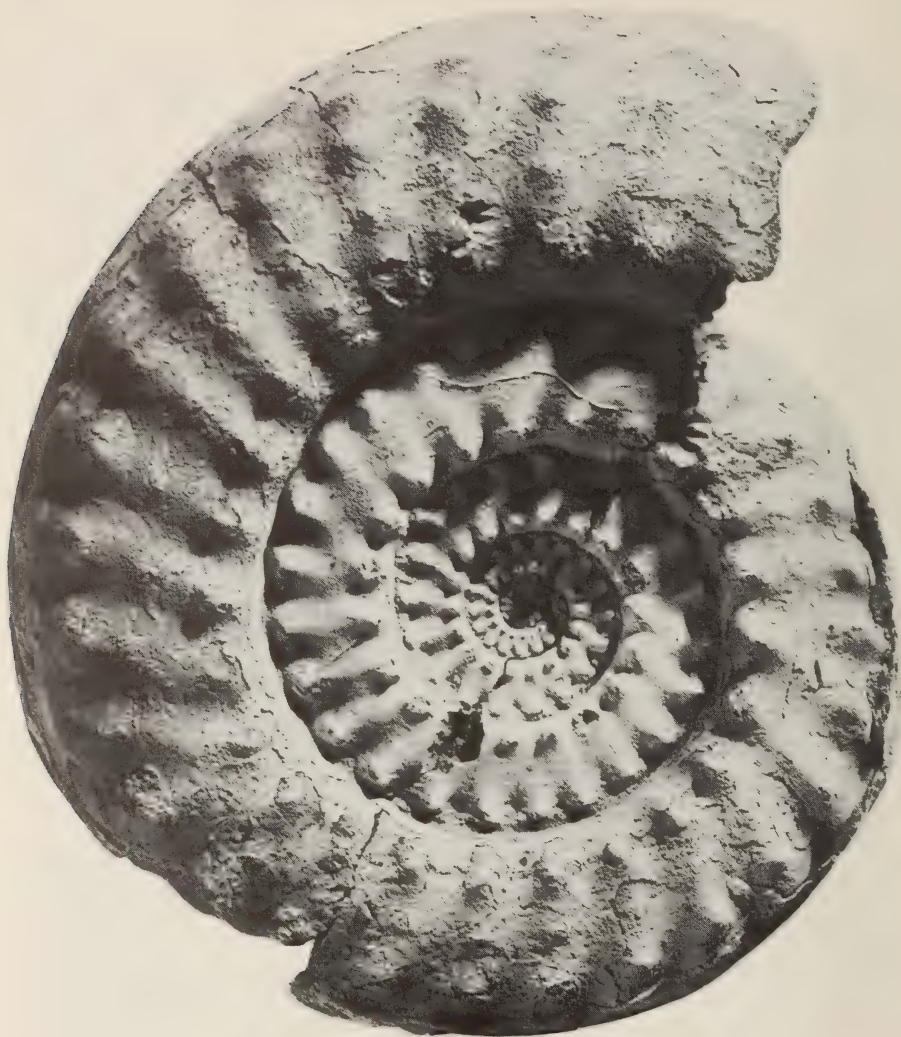


Fig. 59. *Plesiotexanites stangeri* (Baily, 1855). SAM-K5447.  $\times 1$ .

as is its ultimate strength. Lateral tubercles are well developed in BMNH-C19462 (Fig. 61) and C19449 (Fig. 63) compared to the faint lateral tuberculation in BMNH-C19443 (Fig. 60) or BMNH-C19457 (Fig. 66).

#### *Discussion*

This species, together with *Texanites soutoni*, was the first texanitine recorded from the Cretaceous deposits at Umzamba. Even so, it is rather rare in South African collections and the bulk of the material is to be found in the collections of the British Museum (Natural History).



Fig. 60. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19443.  $\times 0,75$ .





Fig. 61. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19462.  $\times 0,75$ .

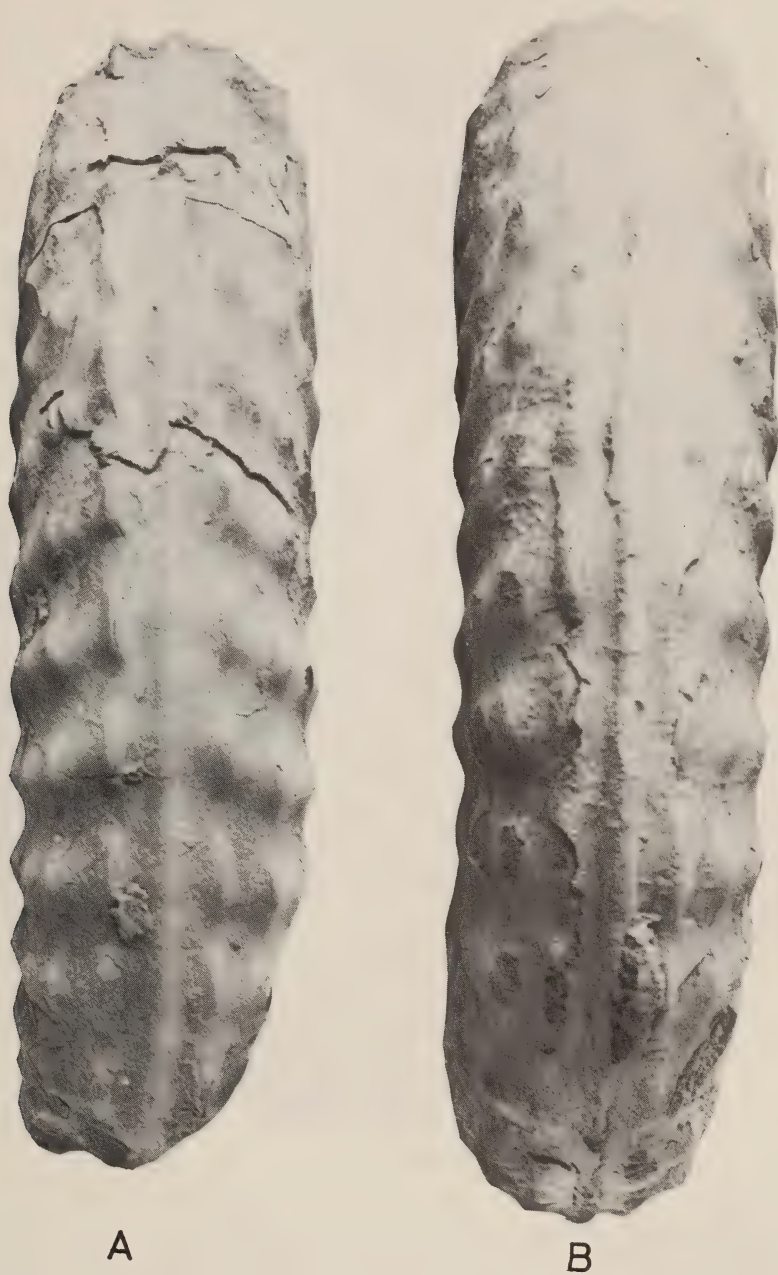


Fig. 62. *Plesiotexanites stangeri* (Baily, 1855). A. BMNH-C19462.  $\times 0,75$ .  
B. BMNH-C19449.  $\times 0,9$ .



Fig. 63. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19449.  $\times 0.7$ .

The type locality of the species was given as 'cliffs off the South African Coast near the Umtafuna and Umzambani Rivers' (Baily 1855: 457). This is currently known as Umzamba Cliff or locality 1 of the authors (Kennedy & Klinger 1975: 281), and is the type section of the authors' Umzamba Formation. Recent collecting by the authors at the type section showed that the known time range of *P. stangeri* in that section is Middle to Upper Santonian, with most





Fig. 64. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19459.  $\times 0.7$ .

occurrences in the Upper Santonian. As far as could be ascertained, there seems to be no stratigraphic difference in occurrence between the varieties *densicosta* and *sparsicosta* or the typical form. These findings seem to be supported by Collignon (1966a) and Young (1963), although the authors doubt if the Malagasy and South African biozonations are compatible with those of the Gulf Coast. Collignon records var. *densicosta* and *sparsicosta* from the Middle Santonian, and var. *densicosta* from the Upper Santonian of Mada-

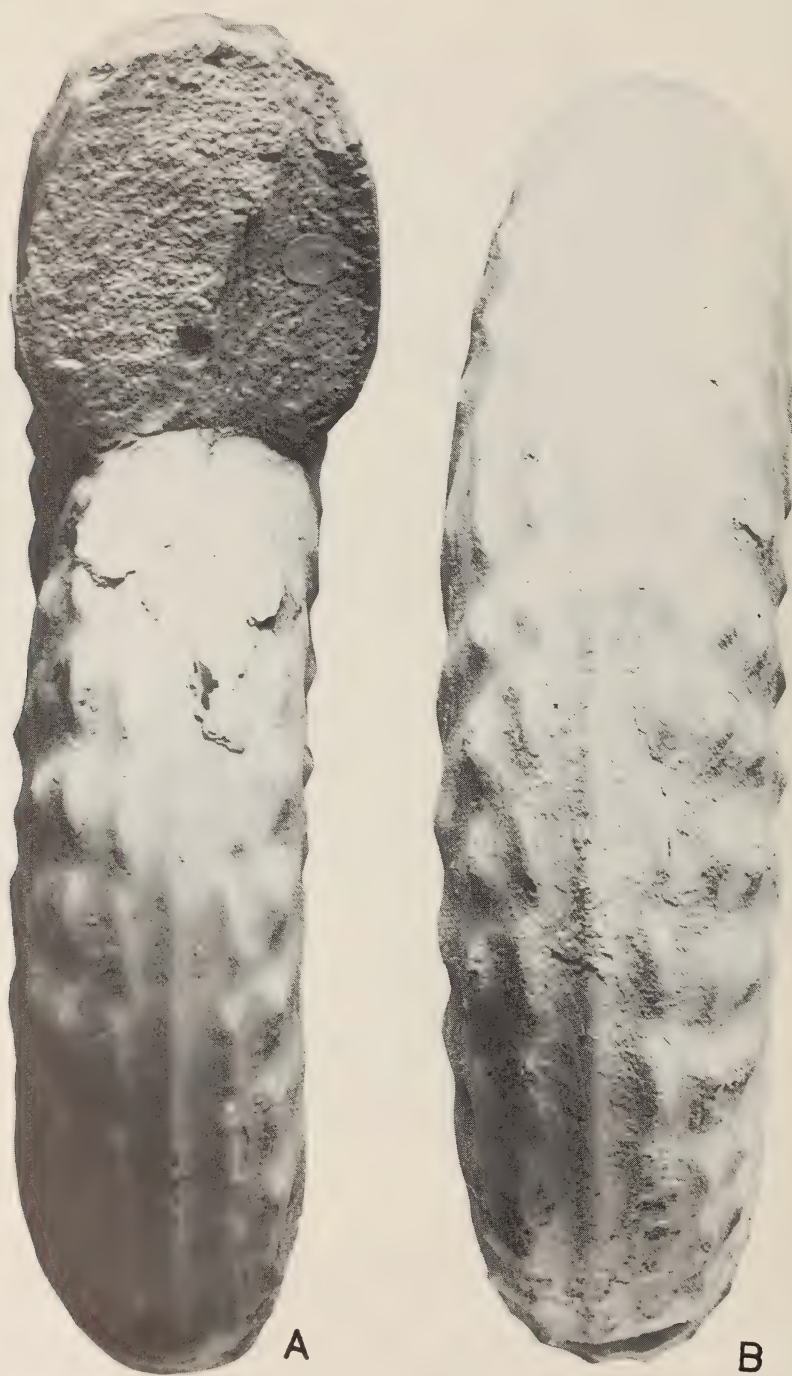


Fig. 65. *Plesiotechanites stangeri* (Baily, 1855). BMNH-C19459.  $\times 0.9$ .

gascar, whereas Young records var. *densicosta* from the Lower Santonian of the Gulf Coast.

In consequence, the authors follow Matsumoto (1970: 288) in here regarding the varietal names as mere convenient morphological terms without taxonomic connotation.

The affinities of the species have already been discussed extensively by Matsumoto (1970) and only little need be added.



Fig. 66. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19457.  $\times 0,8$ .





Fig. 67. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19446.  $\times 1$ .



Fig. 68. *Plesiotexanites stangeri* (Baily, 1855). BMNH-C19450.  $\times 0,75$ .

The external (5) tubercles of some specimens of *P. stangeri* are extremely elongated, creating the appearance of wavy lateral keels. Spath's (1921: 297) assertion that '*Mortoniceras stangeri* Baily sp. has tricarinate inner whorls', however, is a generalization, as the inner whorls of SAM-K5889 (Fig. 53B-C) show. A single specimen, SAM-PCP5687 (Fig. 93C) tentatively referred below to the genus *Reginaites*, is identical to *P. stangeri* in all respects except for possession of two distinct continuous lateral keels at a relatively large diameter.

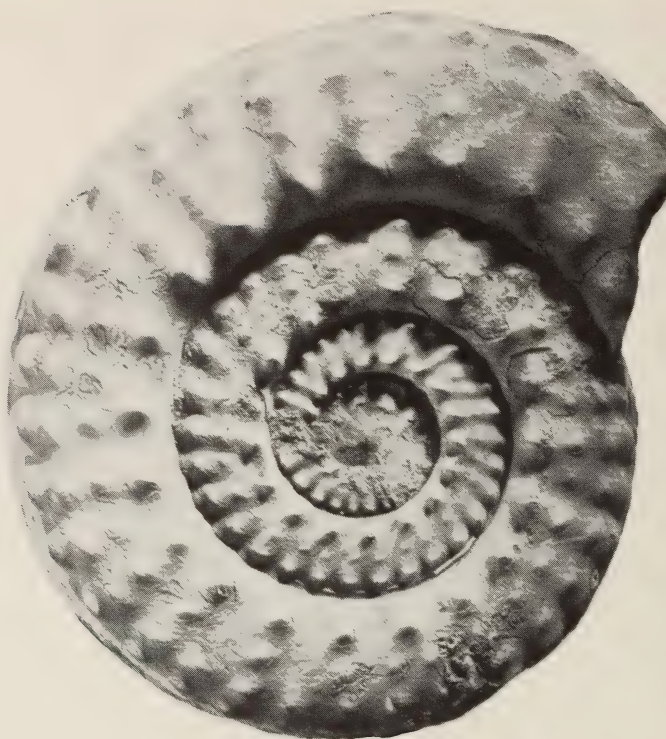


Fig. 69. *Plesiotexanites stangeri* (Baily, 1855). SAM-K4827.  $\times 0,6$ .  
The specimen figured by Woods (1906, pl. 44 (fig. 1)).

Baily's figure of the holotype is reversed and somewhat reconstructed (see Figs 49–51).

#### Occurrence

The geographic distribution of *P. stangeri* in southern Africa is curious. Specimens are relatively abundant at the Umzamba Estuary, while a few specimens are known from subsurface deposits at Durban and Richards Bay and in isolated exposures near Umkwelane Hill.

This appears to be the northernmost occurrence of the species in South Africa. A single doubtful specimen, SAS-K1971 (Fig. 53A), is known from locality 74 at Die Rooiwalle at the north-western end of False Bay and another, BMNH-C81533, from the Hluhluwe floodplain. To all appearances, *P. stangeri* seems to be restricted to the shallow water sediments resulting from the southward-progressing post-Lower Coniacian diachronous transgression (Kennedy & Klinger 1971), being most abundant in the Middle and Upper Santonian sediments at the Umzamba Estuary.

Other reports of this species are from the Middle and Upper Santonian



of Madagascar, an unknown horizon, probably Santonian of Hokkaido, Japan, and the Lower Santonian of the Gulf Coast of the United States of America.

*Plesiotexanites collignoniforme* sp. nov.

Figs 70–78

*Holotype*

SAS-Z1789 (Figs 70–71), locality 85, on the south-western shores of False Bay, Zululand, St Lucia Formation, Santonian I.

*Etymology*

Refers to similarity to *Texanites collignoni* sp. nov.

*Material*

Paratypes are SAS-Z1790a–b, Z1791, Z2109, SAS-H100, H201/43–4, BMNH-C81495–6, C81525–8, C81530–31, all from locality 85, on the south-western shores of False Bay, Zululand, St Lucia Formation, Santonian I.

*Dimensions*

|         | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|---------|----------|------------|------------|----------------|-------------|-------------|-------------|
| Z1789   | 222,0    | 58,0(26,1) | 67,0(30,2) | 0,87           | 103,0(46,4) | 37          | 37          |
| Z2109   | 177,0    | 47,0(26,6) | 57,0(32,2) | 0,82           | 80,0(45,2)  | 31          | 31          |
| H201/44 | 127,0    | 32,0(25,1) | 39,0(30,3) | 0,88           | 59,0(46,5)  | 30          | 30          |
| Z1791   | 195,0    | 49,0(25,1) | 59,0(30,3) | 0,88           | 92,0(47,2)  | 28          | 28          |

*Description*

Coiling is very evolute, with an umbilical width of 45 to 47 per cent of the total diameter, and a very shallow dorsal zone of impression. The whorl section is nearly quadrate in the very early stages of growth, but soon becomes higher than wide with a subtrigonal whorl section and little-inflated flanks. Towards the body chamber the flanks become more inflated and the whorl section more rounded (Fig. 72B).

SAS-Z1790a has the inner whorls preserved (Figs 73–74), permitting a study of the ontogeny. The innermost whorls are completely smooth up to a diameter of c. 8 mm; thereafter ventrolateral nodes start appearing in the umbilical seam, and soon broad, flat ribs appear, some with incipient looping. At a diameter of 20 mm umbilical tubercles start appearing at the dorsal ends of these ribs. Ribbing is single throughout. Lateral (2) tubercles appear at a diameter of c. 50 mm. Simultaneously, the ventrolateral (3) tubercles become less spinose, and migrate away from the umbilical suture to reveal a fourth row of tubercles.

With increasing diameter, ribbing becomes stronger, rursiradiate and slightly sinuous, and tuberculation more prominent. Ribbing continues obliquely over the rounded umbilical wall, but very weakly. The umbilical tubercles (1) are situated high up on the umbilical wall, and tend to migrate up



Fig. 70. *Plesiotexanites collignoniforme* sp. nov. Holotype SAS-Z1789.  $\times 0,6$ .

the ventral part of the flanks. The lateral (2) tubercles are situated near the dorsal third of the flanks, and, though weakly developed, appear most prominent due to the strong development of ribbing in this area. The submarginal (3), marginal (4) and external (5) rows of tubercles are situated closer to each other than the first two rows (1 & 2). The marginal and external tubercles tend to be connected by a thickened rib in *Paratexanites* fashion. The intertubercular area on the venter is connected by a swelling, and the faint, undulating keel tends to form a slight tubercle in this area. The external tubercles tend to be connected



Fig. 71. *Plesiotexanites collignoniforme* sp. nov. Holotype SAS-Z1789.  $\times 0,7$ .



spirally by very faint ridges, thus creating a reticulate pattern over the venter, as in *Paratexanites pseudotricarinatum* sp. nov., though weaker.

Towards the body chamber, the ribs become thinner, and the lateral tubercles tend to become absorbed, followed by the umbilical and eventually submarginal tubercles. The keel also becomes much weakened on the body chamber.

The suture is broad with squat saddles and lobes (Fig. 72A).

### Discussion

Barring slight details in density of ribbing, the species shows very little variation, and is easily distinguished by the evolute coiling, slightly sinuous, rursiradiate ribbing, low, indistinct undulating keel, and faint lateral lines connecting the external tubercles and *Paratexanites*-like proximity of the external and marginal rows of tubercles.

This species is morphologically intermediate between *Paratexanites* and *Texanites* in being quinquetuberculate at a relatively small diameter, but in retaining a *Paratexanites*-like ornament near the ventral part of the shell. Here

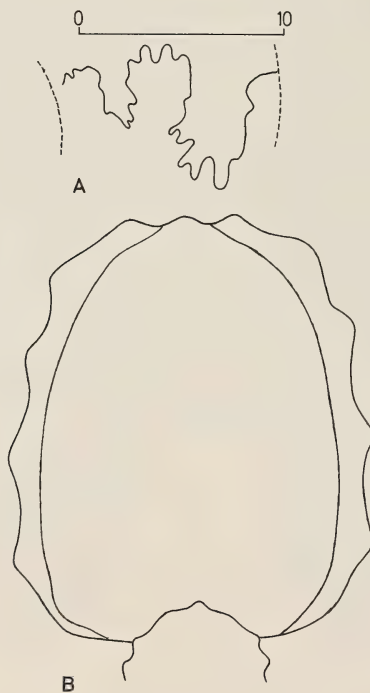


Fig. 72. *Plesiotechanites collignoniforme* sp. nov.  
Paratype SAS-Z1970a. Whorl section and  
partial suture line. Scale bar for suture in millimetres.

distinction between *Texanites* s.s. and *Plesiotechanites* becomes subjective. This species appears to be the source of *Texanites collignoni* and provides a link between *Paratexanites* and *Texanites*. Relative stratigraphic position and similarity of ornament over the venter (undulating keel, reticulate pattern, etc.) leave little doubt as to the origin of the species, namely the plexus of *Paratexanites umkwelanense* and *Paratexanites pseudotricarinatum* sp. nov. Similarly, the whorl section, ornament, especially the rounded umbilical wall with the



Fig. 73. *Plesiotechanites collignoniforme* sp. nov. Paratype SAS-Z1970a.  
× 1.



Fig. 74. *Plesiotechanites collignoniforme* sp. nov. Paratype SAS-Z1790a. Close-up of inner whorls to illustrate early ontogeny.  $\times c. 5$ .

umbilical tubercle situated high up on the flanks, and the undulating keel are reminiscent of *Texanites collignoni* sp. nov. (described below, p. 126), which occurs stratigraphically higher up in the sequence. Similarly, *Texanites texanum* s.l., also with undulating keel, may be derived from this species.

*P. collignoniforme* sp. nov. has a geographically separated, slightly younger relative in *T. umzambiense* sp. nov. (described below, p. 167) from near the base of the Umzamba Formation at its type section. In the latter, the external and marginal tubercles are still approximated, and the keel is still undulating, but the lateral tubercles appear a little earlier, and the whorl section is more





Fig. 75. *Plesiotexanites collignoniforme* sp. nov. Paratype SAS-H100/1.  $\times 1$ .



Fig. 76. *Plesiotexanites collignoniforme* sp. nov. Paratype SAS-H100.  $\times 1$ .



Fig. 77. *Plesiotexanites collignoniforme* sp. nov.  
Paratype SAS-H100.  $\times 1$ .



inflated on the phragmocone. The isolation of the texanite faunas between Zululand and Pondoland could possibly have begun here.

Comparisons with other species are:

- P. stangeri* lacks the strong lateral ornament of *P. collignoniforme* and has a more depressed whorl section.
- P. matsumotoi* sp. nov. has very strongly developed ventrolateral spines or nodes in the early to middle stages of growth, and develops a lateral tubercle much later.
- P. kawasaki* (Kawada) (see especially Matsumoto 1970, pl. 43 (fig. 1)) has dense, thin ribbing on the body chamber similar to the holotype of *P. collignoniforme*, but has much coarser ornament on the inner whorls.
- P. schlueteri* Matsumoto bears some similarity to *P. collignoniforme*, but has a very short *Texanites*-like stage.



Fig. 78. *Plesiotechanites collignoniforme* sp. nov. Paratype SAS-Z1791.  $\times 0,64$ .

*Occurrence*

Lower Santonian, Santonian I of Zululand.

*Plesiotexanites matsumotoi* sp. nov.

Figs 79–83

*Mortonicerias* aff. *umkwelanensis* Spath, 1921: 234, text-fig. D2.

*Protexanites* (*Anatexanites*) sp. aff. *P. (A) nomii* Klinger & Kennedy 1977: 98, figs 8B–E, 10A, 11.

*Holotype*

SAM–PCP5683, Bed B7 locality 1, southern side of the Umzamba Estuary, Pondoland, Transkei, Umzamba Formation, Santonian II.

*Etymology*

Named for Professor emeritus T. Matsumoto, Kyushu, Japan.

*Material*

Paratypes are SAS–BH9/121,50 from Upper Santonian borehole material near Richards Bay; SAM–5491 from locality 10, Umkwelane Hill, Zululand, St Lucia Formation, Santonian to Campanian; and BMNH–C19451 from an unknown horizon within the Umzamba Formation at the Umzamba Estuary, locality 1, Pondoland, Transkei.

*Dimensions*

|          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|------------|------------|----------------|------------|-------------|-------------|
| SAM–5491 | 240,0    | 71,0(29,6) | 84,0(35,0) | 0,84           | 98,0(40,8) | 15 × 2      | 15 × 2      |
|          | 170,0    | 60,0(35,3) | 61,0(35,9) | 0,98           | 72,0(42,4) | —           | —           |
|          | 102,0    | 36,0(35,3) | 37,0(36,3) | 0,97           | —          | 10 × 2      | 10 × 2      |

*Description*

Coiling is evolute, with an umbilical diameter of 40 to 46 per cent of the total diameter. The whorl section is angular in the early stages, becoming more rounded on the outer whorls. On the inner whorls, the section is subrectangular, broader than high, but with increasing growth the section becomes higher than wide, with a broadly rounded venter and no distinct umbilical wall.

Ontogenetic development can be seen in SAM–PCP5683 (Fig. 79). The very innermost whorls are not preserved, but at a diameter of 5 mm the whorl section is round, with slight swellings in the umbilical wall. From 5 to 8 mm diameter, strong, spinose ventrolateral spines which lean against the umbilical wall start appearing. Beyond 8 mm, low, rounded ribs corresponding in number to the ventrolateral spines appear, and at 12 mm the first small umbilical (1) tubercles are visible. Beyond that diameter, ornament becomes stronger, consisting of very strong ventrolateral spines, leaning against the umbilical wall and smaller, slightly inward-pointing umbilical tubercles, connected by low,

broad ribs numbering about 15 per whorl (Fig. 79). Occasional small, yet distinct intercalatory umbilical tubercles not associated with any ribs or ventrolateral spines occur. Very faint lateral (2) tubercles start appearing at a diameter of *c.* 60 to 70 mm, becoming increasingly stronger with growth. At this diameter the ventrolateral ornament is fully exposed on the holotype. The ventrolateral (3+4) tubercles are no longer spinose, but appear as prominent rounded bosses, indicating that the original spines became detached at a basal septum. The external (5) tubercles are distinctly separated, though very elongated. The central keel is lower than the train of external tubercles and appears smooth.

At diameters between 70 and 80 mm, the strong ventrolateral (3+4) nodes begin to show a tendency towards doubling, with the formation of a small clavate marginal tubercle (4), and a larger, rounded submarginal (3) tubercle. This eventually leads to the development of a normal quinquetuberculate *Texanites* ornament as shown by SAM-5491 (Figs 80B-81), although the lateral tubercle is never very well developed.

On the later part of the phragmocone the tubercles are virtually equidistant. The umbilical ones are pointed and radially elongated; the lateral ones small and conical, and the submarginal, marginal and external ones clavate in ascending order. On the last part of the phragmocone and on the body chamber all ornament weakens considerably, and ribs become very narrow (Fig. 81).

### Discussion

In the authors' (Klinger & Kennedy 1977) previous description of part of the present material, the eventual splitting of the ventrolateral node was not noticed due to incomplete exposure; hence their tentative reference to *Protexanites* (*Anatexanites*). The Umkwelane Hill and some Pondoland specimens, however, clearly show the *Plesiotexanites* affinity of the material.

The inner whorls resemble those of *Paratexanites australis* sp. nov., and this species can possibly be derived from the latter. The spinose ventrolateral nodes which remain undivided for a great distance are common to both species.

Further comparisons may be made with *Plesiotexanites kawasakii* (Kawada), but in this species the ventrolateral spines are divided into weak inner and stronger outer tubercles at the onset of the appearance of the lateral tubercle. Thus the quinquetuberculate stage follows immediately after the trituberculate stage, whereas *Plesiotexanites matsumotoi* has a quadrituberculate *P.* (*Anatexanites*)-like stage before the quinquetuberculate stage.

*P. thomsoni* (Jones), of Upper Coniacian or Lower Santonian age, is similar in retaining a quadrituberculate stage to a large diameter (200 mm +) before the quinquetuberculate stage, but differs considerably in ornament and general shape. In *P. thomsoni* there is a marked decrease in size of umbilical and ventrolateral tubercles at the onset of the appearance of the lateral (2) tubercles, which does not happen in *P. matsumotoi* sp. nov., and it also has much finer, denser costation than the latter.





Fig. 79. *Plesiotexanites matsumotoi* sp. nov. Holotype SAM-PCP5683.  $\times 1$ .



Fig. 80. *Plesiotexanites matsumotoi* sp. nov. A. Holotype SAM-PCP5683.  
B. SAM-5491. A  $\times 1$ ; B  $\times 0,5$ .

The weak, occasional intercalated umbilical nodes in *P. matsumotoi* are also possibly of specific significance.

*P. collignoniforme* sp. nov. has a slower rate of expansion, and is more weakly ornamented throughout, than *P. matsumotoi*.

There is slight superficial resemblance to *Paratexanites umkwelanense* as Spath (1921: 234) had probably implied in referring the large specimen, SAM-



Fig. 81. *Plesiotexanites matsumotoi* sp. nov. SAM-5491. This is the specimen originally described by Spath (1921: 234) as *Mortonicerias* aff. *umkwelanense*.  
× 0,52.

5491, tentatively to that species. The presence of lateral tubercles, however, clearly precludes inclusion of this specimen in *Paratexanites*.

This species is of additional importance in that it seems to connect to the *Reginaites* species described below (p. 111).

#### *Occurrence*

Middle to Upper Santonian of Pondoland, and Zululand.





Fig. 82. *Plesiotexanites matsumotoi* sp. nov. Paratype BMNH-C19451. (British Museum photograph.)  $\times 1$ .



Fig. 83. *Plesiotexanites matsumotoi* sp. nov. Paratype BMNH-C19451.  
(British Museum photograph.)  $\times 1$ .

*Plesiotexanites?* sp. indet.

Fig. 84

*Material*

A single specimen, SAS-76B from locality 74, north-western end of False Bay at Die Rooiwal, Zululand, St Lucia Formation, Santonian I to Campanian I.

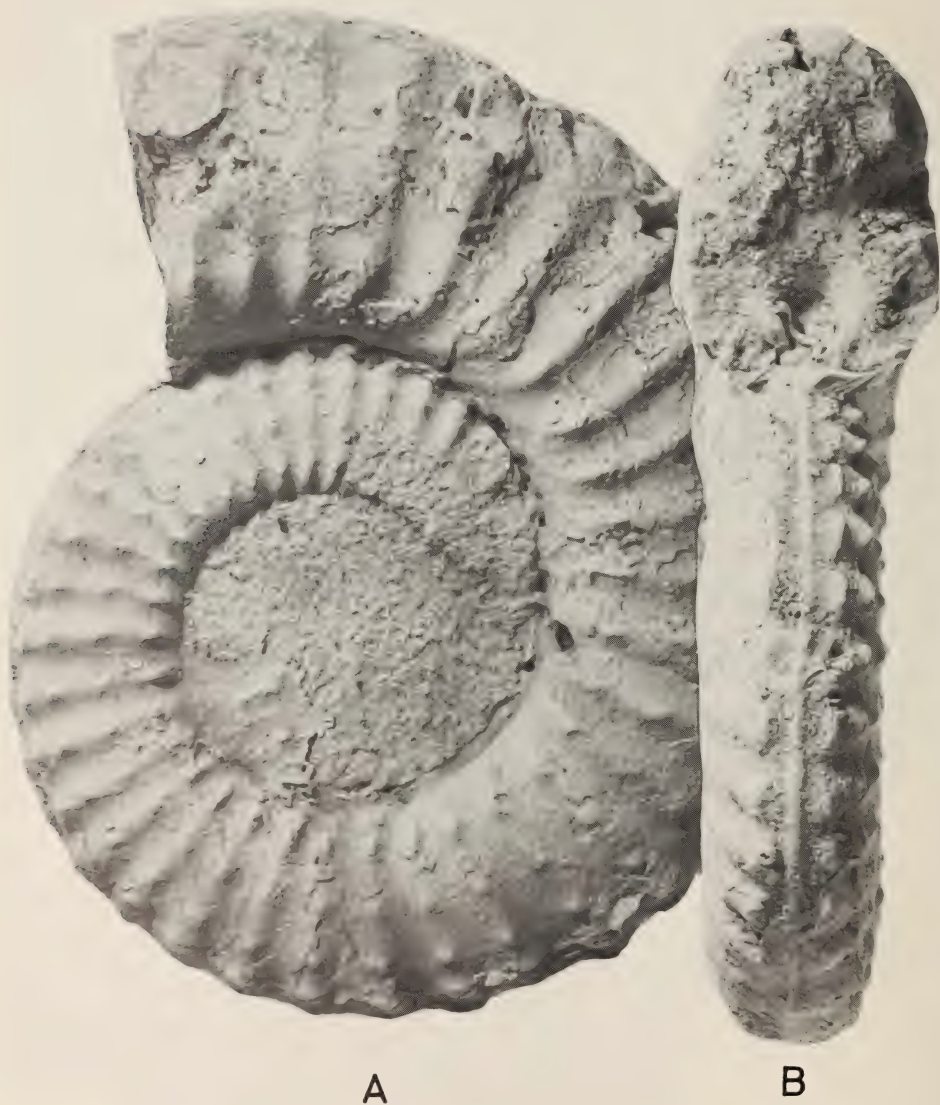


Fig. 84. *Plesiotexanites?* sp. indet. SAS-76B.  $\times 0.8$ .



*Dimensions*

| <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|----------|------------|------------|----------------|------------|-------------|-------------|
| 166,0    | c.40(c.24) | c.54(c.32) | c.74           | 76,0(45,8) | 33          | 33          |

*Description*

The available specimen is septate throughout, and lacks the inner whorls. Coiling is evolute, with an umbilical diameter of 45,8 per cent. The whorl section is distinctly higher than wide, with a very shallow dorsal zone of impression, widely rounded umbilical wall passing into weakly inflated flanks without giving rise to a distinct umbilical edge, and with a narrow, rounded venter. Ornament is weak throughout, consisting of widely spaced (c. 33 per whorl), gently forwardly curved single ribs bearing five feeble rows of tubercles. The umbilical (1) tubercles appear to arise in the umbilical wall, and are small and radially elongated. The lateral (2) tubercles are smallest, conical, and situated just dorsad of midflank. The submarginal (3), marginal (4) and external (5) rows are progressively clavate, and situated closer to each other than the other rows. The keel is inconspicuous and much lower than the external tubercles.

The suture line is unknown.

*Discussion*

Lacking the inner whorls, it is uncertain whether this specimen is referable to *Texanites* or to *Plesiotexanites*. The very weak ornament and compressed whorl section is totally different from any of the other texanite species available in South Africa. On account of the weak development of the lateral tubercles and the proximity of the ventral three rows of tubercles, the specimen is very tentatively referred to *Plesiotexanites*.

As far as looseness of coiling is concerned, there is some similarity to *P. stangeri*, but the latter has a more angular whorl section and stronger ornament.

In terms of relative proportions, the Zululand specimen falls within the limits of *Texanites venustus* Collignon (see Collignon 1966a: 74, pl. 485 (fig. 1960)) and *Texanites hourcqi* var. *souromarayensis* (see Collignon 1966a: 74, pl. 485 (fig. 1959)), both from the Middle Santonian of Madagascar, but lacks the bifurcating ribs of these two species.

*Occurrence*

Santonian of Zululand.

Genus *Reginaites* Reymont, 1957

(?= *Reymentites* Matsumoto, 1965)

*Type species*

*Peroniceras* (*Reginaites*) *quadrituberculatum* Reymont (1957, pl. 11 (fig. 1a-b), text-fig. 7) by the original designation of Reymont (1957: 65).

*Diagnosis*

Coiling evolute. Venter generally tricarinate throughout, but early whorls may possibly have wavy lateral keels. Central keel stronger than lateral keels. Ornament on the flanks in early stages is bituberculate; umbilical (1) and ventrolateral (3+4). With increasing diameter, the ventrolateral tubercles divide into a row of clavate marginal (4) and a more rounded row of sub-marginal (3) tubercles. Lateral (2) tubercles appear later, or not at all, and are generally weaker than the other tubercles. Towards the body chamber, ornament may weaken. The suture is of collignoniceratid type, with little-incised elements.

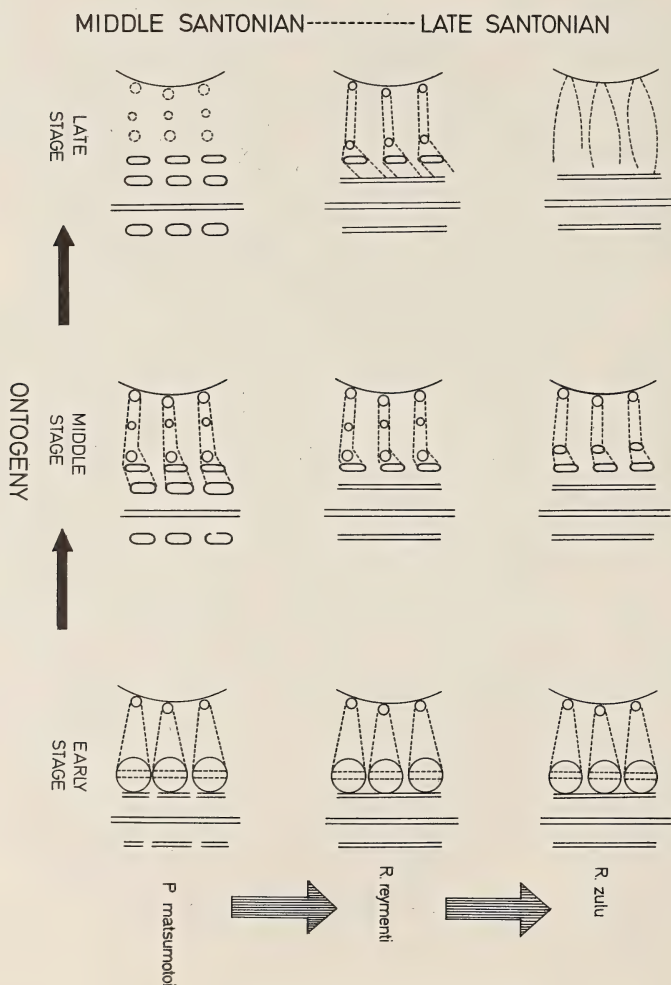


Fig. 85. Diagram to illustrate probable evolutionary relationship and known ontogenetic changes in South African representatives of genus *Reginaites*.

### Discussion

*Reginaites* poses difficulty in interpretation, being poorly represented in numbers. Reyment (1957: 65) introduced the genus as a subgenus of *Peroniceras*, based on a single specimen from the Asu River, near Agbani, Nigeria, then believed to be of Upper Coniacian age. Apart from the type species, here reproduced as Figures 87C, 89, Reyment also included *Peroniceras leei* Reeside 1927: 40, pl. 42 (figs 1–2), pl. 43 (figs 3–4)), a Lower Campanian species, in *Reginaites*. Young (1963: 92) added another species, *Reginaites durhami*, from the base of the Lower Campanian, to the genus.

Since then, however, new taxa have been erected for species with tricarinate venters and simple collignoniceratid suture, thus obscuring differences between the Texanitinae and Peroniceratinae, and also within the latter.

These taxa are:

*Fraudatoroceras* van Hoepen, 1965 (type species *Fraudatoroceras besairiei* van Hoepen, 1965a: 36, pl. 27, text-fig. 9a–b) from the Coniacian of Zululand.

*Cobbanoceras* Matsumoto, 1965 (type species *Cobbanoceras tanakai* Matsumoto, 1965: 220, pl. 37 (fig. 3), pl. 38 (fig. 1), pl. 39 (fig. 1) text-figs 4–5) from the Santonian of Hokkaido and ?Coniacian of California.

*Reymentites* Matsumoto, 1965 (type species *Reymentites hataii* Matsumoto 1965: 240, pl. 42 (fig. 3), text-figs 19–20) from the Urakawan (Coniacian and Santonian) of Hokkaido.

As far as diagnoses are concerned, *Fraudatoroceras* van Hoepen and *Cobbanoceras* Matsumoto appear to be synonymous. Both are tricarinate, bituberculate, widely umbilicate and have simple sutures similar to those of *Gauthiericeras* (see Van Hoepen 1965a: 35–6; Matsumoto 1965: 219–220). If the taxa are, indeed, the same, *Cobbanoceras* is a junior synonym of *Fraudatoroceras*, as Van Hoepen's work precedes that of Matsumoto by four months (27 July 1965 v. 20 November 1965). Full details are to be given in the authors' pending revision of the Peroniceratinae.

According to Matsumoto (1965: 239) *Reymentites* resembles *Reginaites* in being trituberculate or quadrituberculate, but differs from the latter in having the tubercles spaced more or less equidistant, rather than having the ventrolateral tubercles (3+4) situated close together. This relationship would thus be somewhat analogous to that between *Paratexanites* and '*Parabevahites*'. The holotype, and, indeed, only individual available of *Reymentites hataii*, is a wholly septate individual and probably immature, but does show the equidistant tuberculation. Apart from the latter species, Matsumoto (1965: 239) also referred *Reginaites durhami* Young to genus *Reymentites*. The holotype of this species lacks the inner whorls, and the equidistant tuberculation present may well be regarded as the normal result of ontogenetic change in *Reginaites* as here interpreted. *Reymentites* is thus provisionally included in the synonymy of *Reginaites*, contrary to the views of Wiedmann (1978: 670).



Species which may thus be referred to *Reginaites* are:

- Reginaites durhami* Young (1963: 92, pl. 39 (fig. 2), pl. 49 (figs 1–2, 4), text-fig. 22bc) from the Lower Campanian of the Gulf Coast of North America.  
*Reginaites gappi* Wiedmann (1978: 668, pl. 3 (figs 1–3), text-figs 2c, 3b) from the Upper Santonian of Austria.  
*Reymentites hataii* Matsumoto (1965: 240, pl. 42 (fig. 3), text-figs 19–20) from the Urakawan (Coniacian and Santonian) of Hokkaido.  
*Reginaites leei* (Reeside) (1927: 40, pl. 42 (figs 1–2), pl. 43 (figs 3–4)) from the Lower Campanian of New Mexico.  
*Reginaites quadrituberculatum* Reyment (1957: 65, pl. 11 (fig. 1a–b), text-fig. 7) from the Upper Coniacian? of Nigeria.

To this list may be added two new species:

- Reginaites reymenti* sp. nov. from the Upper Santonian or Lower Campanian of Zululand.  
*Reginaites zulu* sp. nov. from the top of the Upper Santonian of Zululand.

Specific differentiation between the species is based mainly on the whorl section, presence or absence of lateral (2) tubercles and stage of splitting (if at all) of the ventrolateral tubercle and ornament on the body chamber.

Unfortunately, dating of all the species is not satisfactory. *Reymentites hataii* cannot be dated more accurately than Urakawan (Coniacian and Santonian). *Reginaites leei* and *R. durhami* are of definite Lower Campanian age, whilst the Zululand specimens are not older than Upper Santonian. The holotype of *R. quadrituberculatum* was collected by R. Blaser in beds above undoubted Coniacian and was thus tentatively dated as Upper Coniacian. According to Reyment (pers. comm. 21 November 1977), however, there is no evidence to gainsay a Santonian age for this species, and in the light of the present knowledge this would be a more reasonable alternative.

Thus, unless we are here dealing with a polyphyletic group, or heterochronous homoeomorphic groups, *Reginaites* seems to be a Santonian to Lower Campanian genus.

Similarities between *Reginaites* and *Plesiotexanites* are striking. Apart from the presence of lateral keels versus an external (5) row of tubercles, there is no significant difference. This similarity had already been remarked upon by Young (1963: 93).

As in other known occurrences, *Reginaites* does not occur in great numbers in Zululand, but from the specimens available, a phylogenetic sequence as outlined in Figure 85 could be envisaged. *Plesiotexanites matsumotoi* sp. nov., with large ventrolateral spines or nodes, appears most suitable as ancestral form in South Africa. Through further lengthening of the already long external tubercles, the tricarinate venter is obtained. The ventrolateral (3+4) tubercles remain intact to greater diameters and the lateral (2) tubercle appears later and eventually not at all, thus giving rise to *Reginaites zulu* sp. nov. via *R. reymenti* sp. nov. A further possible trend is that the central keel becomes

progressively more prominent at expense of the lateral keels and the venter more fastigate, as in *R. zulu*. From this it would be possible to connect to *Neogauthiericeras*.

Matsumoto (1965: 240) suggested that *Reginaites*, *Reymentites* and *Cobbanoceras* may be grouped together in a new subfamily. In view of the close similarity and relationship between *Plesiotexanites* and *Reginaites*, however, separation at this level is unacceptable, even if this inclusion deviates from the unicarinate character of the rest of the texanitids.

#### *Occurrence*

Stratigraphic data on *Reginaites* species are still confusing, as discussed above. Current data seem to indicate that the genus is restricted to the Santonian to Lower Campanian of Austria, Nigeria, Gulf Coast of North America, Hokkaido, Zululand, and, questionably, Pondoland.

#### *Reginaites reymenti* sp. nov.

Figs 86, 87A–B, 88

#### *Holotype*

SAS-Z1986 (Fig. 87A–B), locality 74, Die Rooiwalle, Zululand, St Lucia Formation, Santonian I to Campanian I. \*

#### *Etymology*

Named for Professor R. A. Reyment, Uppsala.

#### *Material*

Paratypes are SAM-PCZ5877, PCZ5887–PCZ5888 from an unlocalized collection, but presumably also from Die Rooiwalle, as is the holotype.

#### *Description*

All the specimens are fragmentary, but together give a good idea of a complete individual.

Coiling is evolute, with an umbilical diameter of about 44 per cent. The whorl section in the early whorls is rectangular, wider than high, but becomes more inflated with a rounded venter in later whorls, resulting in a dome-shaped, but still wider than high whorl section.

On the earliest whorls preserved, at a diameter of *c.* 30 mm, ornament consists of small, pointed, conical, to radially elongated umbilical (1) tubercles, and strong, bullate, slightly clavate ventrolateral nodes connected by low, broad, widely-spaced single ribs. The venter has three keels of which the central one is strongest. At larger diameters, the ventrolateral nodes begin dividing into two: a rounded submarginal (3) node and a smaller, clavate marginal (4) tubercle. The first sign of division appears at *c.* 60 mm diameter.

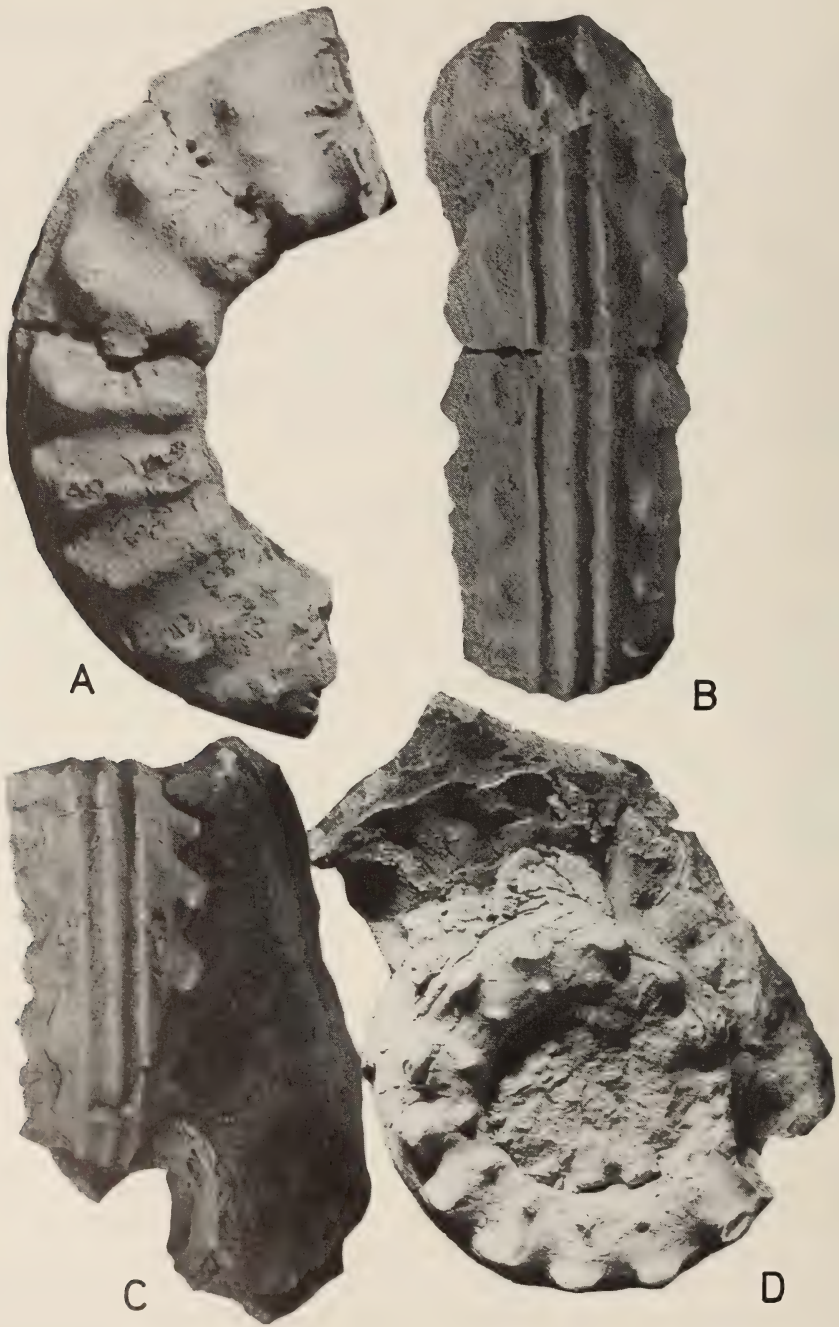


Fig. 86. *Reginaites reymenti* sp. nov. A-B. Paratype SAM-PCZ5877. C-D. Paratype SAM-PCZ5887. Note the faint lateral tubercle on the upper end of A.  $\times 1$ .



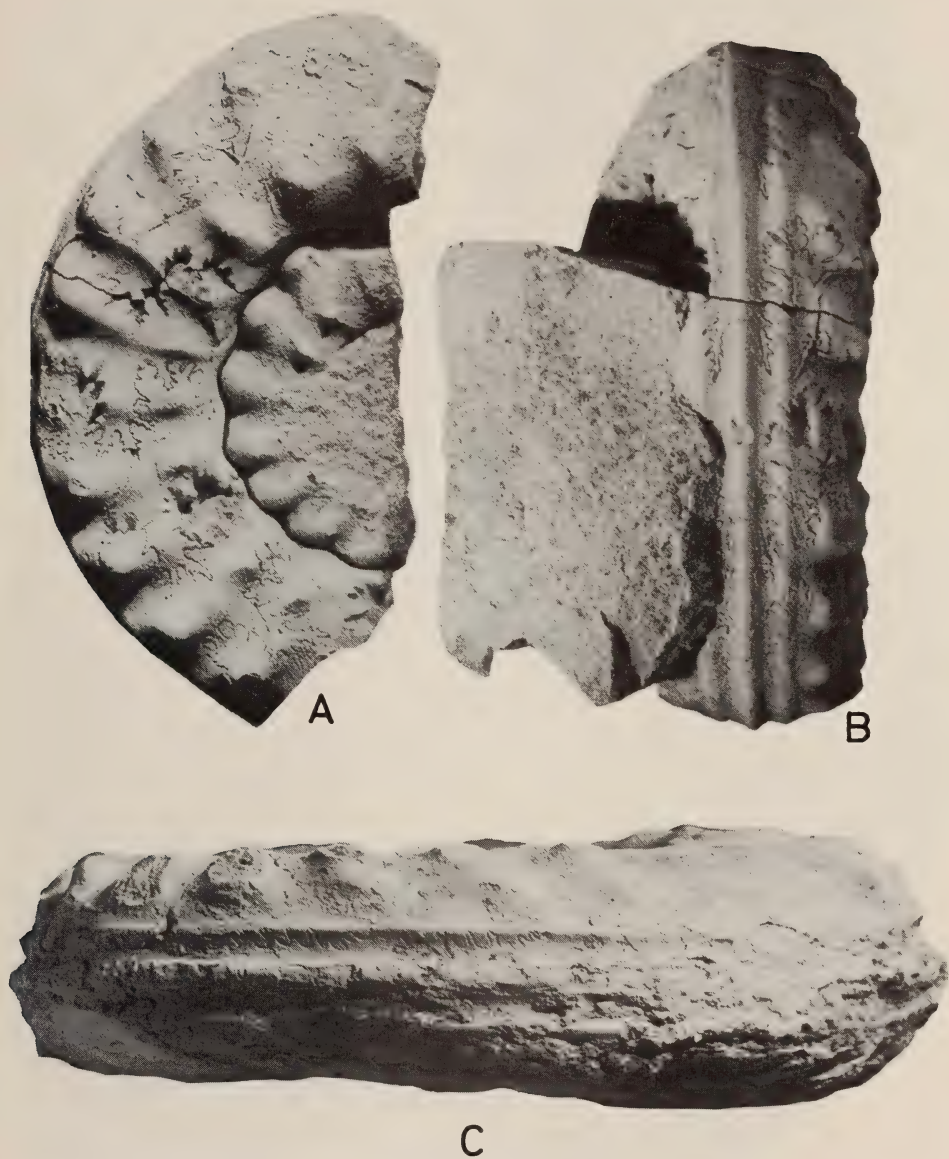


Fig. 87. A-B. *Reginaites reymonti* sp. nov. Holotype SAS-Z1986. C. *Reginaites quadrituberculatum* Reymont, 1957. Holotype BMNH-C48040.  $\times 1$ .

On specimens SAM-PCZ5877 and SAS-Z1986 (Figs 86A-B, 87A-B), which illustrate development at larger diameters, ribbing becomes prorsiradiate, the marginal (4) tubercle migrates forward, ahead of the submarginal (3) tubercle on the venter. Further development differs somewhat in these two specimens. At the largest diameter preserved on SAS-Z1986 (Fig. 87A-B), ornament remains trituberculate, i.e. umbilical (1), submarginal (3) and marginal



Fig. 88. *Reginaites reymonti* sp. nov. Paratype SAM-PCZ5888. Showing part of body chamber with sharpened ribbing.  $\times 1$ .



Fig. 89. *Reginaites quadrituberculatum* Reyment, 1957. Holotype BMNH-C48040.  $\times 1$ .



(4). On SAM-PCZ5877 (Fig. 86A-B), however, which is of similar size to the outer whorl of the holotype, a small but distinct lateral (2) tubercle appears. In SAM-PCZ5888 (Fig. 88), which probably belongs to the same individual as the former specimen (SAM-PCZ5887), part of the body chamber is preserved. Here, all the tubercles tend to become incorporated in the ribbing, which becomes sharper and apparently more distantly spaced. The ribs now are prorsiradiate over the flanks, bend sharply forward between the submarginal (3) and marginal (4) tubercles, and then continue as thin riblets up to the lateral keel. Preservation in this specimen is rather poor but it does appear that the lateral (2) tubercle again disappears on the body chamber, or stays feeble throughout.

### Discussion

This species is characterized by the strong, bullate ventrolateral tubercles on the inner whorls, weak development of the lateral (2) tubercle and tricarinate venter. Development of tuberculation is remarkably like that of *Plesiotexanites*, especially *P. matsumotoi* sp. nov., but in this latter species the ventrolateral tubercles remain undivided up to larger diameters, and the lateral (2) tubercle develops more strongly. Furthermore, *P. matsumotoi* is distinctly unicarinate, being a true texanid. It would, however, be easy to derive *Reginaites reymenti* from *P. matsumotoi* by elongation of the external tubercles to form the lateral keels of *Reginaites*. The variable development of the lateral tubercle is another feature reminiscent of *Plesiotexanites*, as observed in *P. stangeri* (Baily).

*Reginaites zulu* sp. nov. (described below) totally lacks development of the lateral tubercles and remains bituberculate to a much greater diameter.

*Reginaites leei* (Reeside) is imperfectly known, but appears to have weaker ornament. Reyment (1957: 66) states *R. leei* to have lateral tubercles, although Reeside (1927: 40) does not mention any.

*Reginaites quadrituberculatum* Reyment, here shown as Figures 87C, 89, has similar ornament on the inner whorls, but has a more compressed whorl section.

*Reginaites durhami* Young has a whorl section much higher than wide throughout, as has *Reginaites gappi* Wiedmann.

### Occurrence

Probably Upper Santonian or Lower Campanian of Zululand.

### *Reginaites zulu* sp. nov.

Figs 90-92, 93A-B, 94

### Holotype

SAS-H126A/9 (Figs 90A-B, 91-92, 93A-B), Bed 1 locality 105, south-eastern shores of False Bay, Zululand, St Lucia Formation, Upper Santonian.

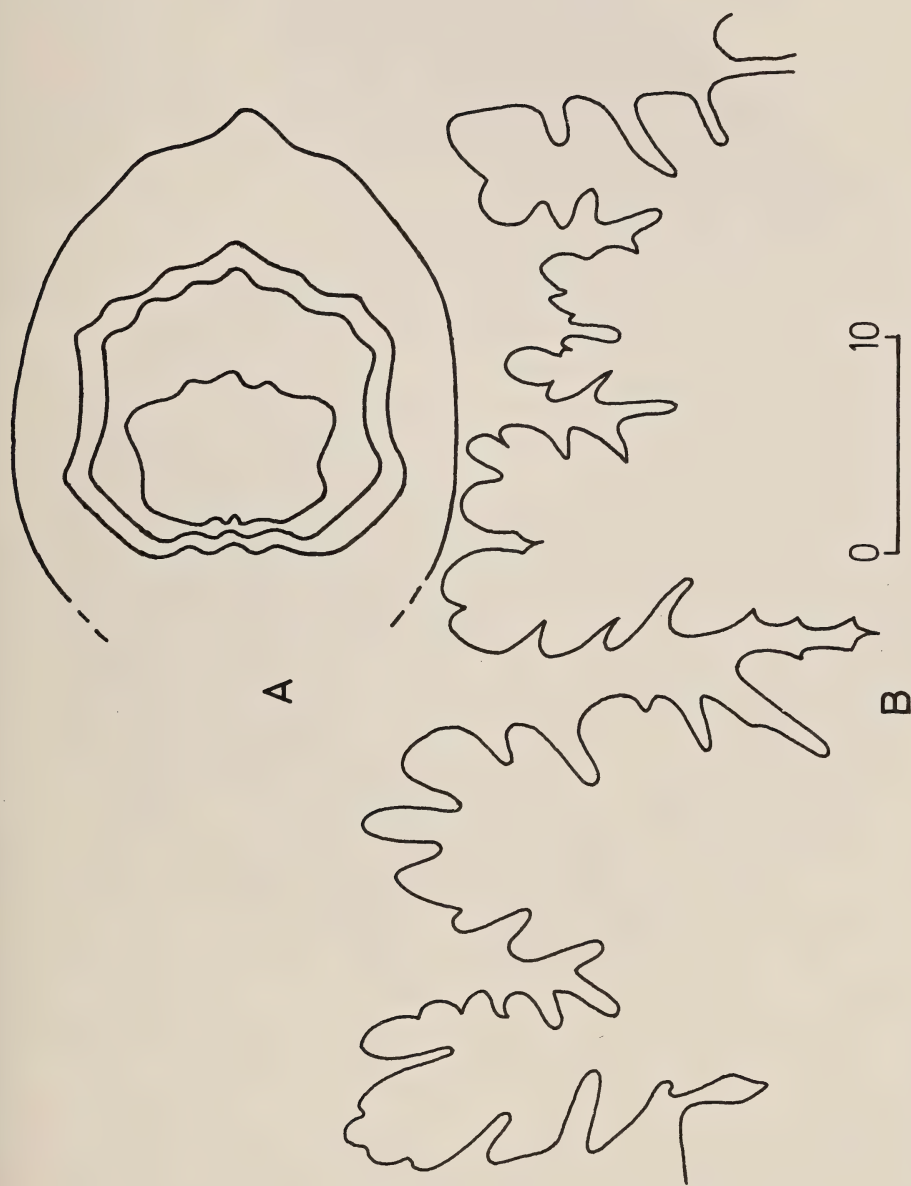


Fig. 90. *Reginaites zulu* sp. nov. A. Whorl section of successive stages of the holotype, SAS-H126A/9, and paratype SAS-H126A/4. B. Suture line from holotype. Scale bar in millimetres.



Fig. 91. *Reginaites zulu* sp. nov. Holotype SAS-H126A/9.  $\times 1$ .

*Etymology*

Named after the original inhabitants of Zululand.

*Material*

Paratype is a single body chamber fragment, SAS-H126A/4 from the same locality and horizon as the holotype, and possibly belongs to the same specimen.



*Dimensions*

|         | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   |
|---------|----------|------------|------------|----------------|------------|
| H126A/9 | 140,0    | 38,7(27,6) | 40,0(28,6) | 0,96           | 74,0(52,9) |

*Description*

Coiling is very evolute, with an umbilical width of 52 per cent. The whorl section varies during ontogeny, changing from subrectangular, higher than wide on the inner whorls, through subsquare with a fastigate venter in the late phragmocone to distinctly higher than wide on the body chamber (Fig. 90A).

The innermost whorls are not preserved, but at a diameter of *c.* 55 mm, ornament consists of a row of conical umbilical (1) tubercles connected by low, broad, prorsiradiate ribs to bullate, slightly spirally elongated ventrolateral (3+4) nodes. The venter is distinctly tricarinate, with the central keel strongest. At a diameter of *c.* 65 mm the ventrolateral (3+4) node starts showing signs of division by the formation of a clavate node (4) on the ventral side. With increasing diameter the separation becomes progressively more obvious, and simultaneously, ornament in general becomes weaker, and the venter distinctly fastigate, as seen at the largest diameter preserved on the holotype. No sign of lateral (2) tubercles is present at this diameter, and it is assumed that they are absent throughout. Rib density is nineteen per whorl.

A large body chamber fragment, SAS-H126A/4 (Fig. 94A-B) from the same locality and horizon as the holotype, has a distinct tricarinate keel, and is here regarded as representing the adult stage of the species. The whorl section is distinctly higher than wide, and, barring a few faint, broad undulations on the flanks, devoid of lateral ornament.

The suture line is simple, with a long, narrow, bifid asymmetrically lateral lobe (L.) (Fig. 90B).

*Discussion*

This species is identified by the apparent lack of a lateral (2) tubercle throughout, presence of a distinctly fastigate venter in later stages of growth, and loss of ornament on the body chamber.

*Reginaites zulu* is allied to *R. reymenti* sp. nov. in earlier stages of growth, but differs in later stages of growth in whorl section and ornament.

*R. durhami* is superficially similar in becoming less strongly ornamented in later stages of growth, but has a distinct lateral tubercle on the phragmocone.

The ontogenetic change in ornament and whorl section of *R. zulu* sp. nov. is analogous to that of some species of *Yabeiceras*, e.g. *Y. orientale* (Matsumoto *et al.* 1964: 326, fig. 2a-e).

The fastigate venter on the late phragmocone and the early bituberculate ornament of *R. zulu* is very much like that of *Neogauthiericeras zafimahovai* Collignon from the basal Campanian of Madagascar. It could be argued that through retention of the bituberculate stage throughout, and earlier acquisition of a fastigate venter and loss of the lateral keels, *R. zulu* could give rise to

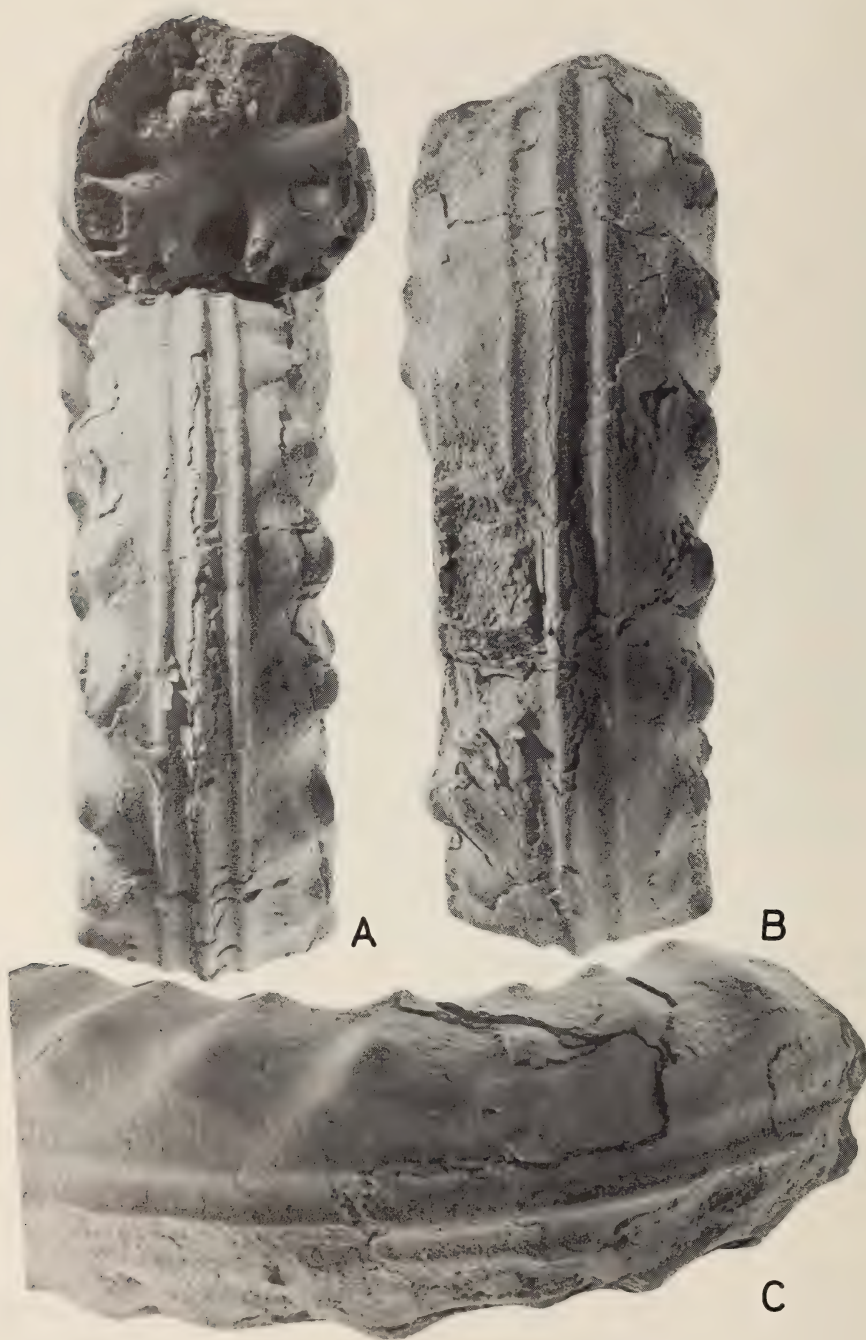


Fig. 92. *Reginaites zulu* sp. nov. Holotype SAS-H126A/9.  $\times 1$ .

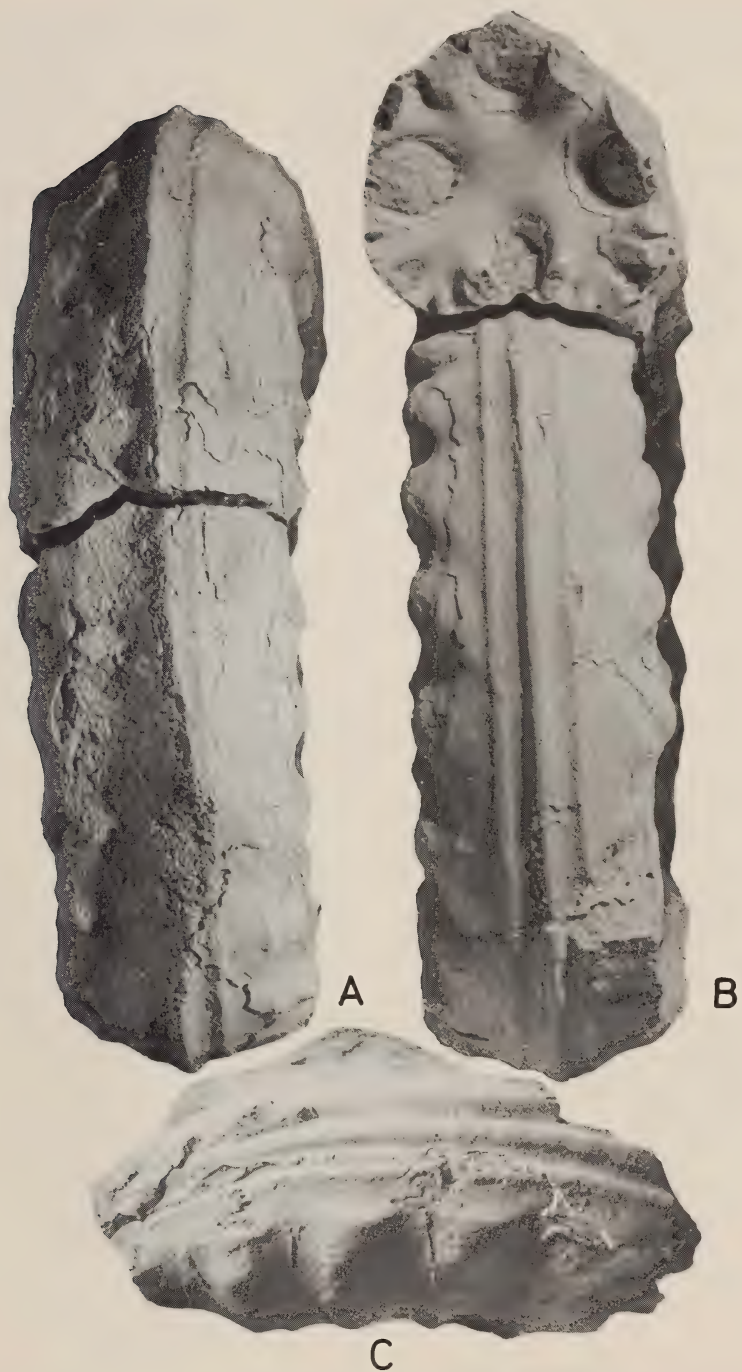


Fig. 93. A-B. *Reginaites zulu* sp. nov. Holotype with part of phragmocone added (also shown in Fig. 92C). C. *Reginaites?* sp. nov.? cf. *Plesiotexanites stangeri* (Baily, 1855).  $\times 1$ .



*N. zafimahovai*. The respective stratigraphic occurrences of the two species (Upper Santonian and basal Campanian) favour this relationship, but additional material is needed to confirm it.

#### *Occurrence*

Upper Santonian of Zululand.

*Reginaites*? sp. nov.? cf. *Plesiotexanites stangeri* (Baily, 1855)

Fig. 93C

#### *Material*

SAM-5687 and SAM-K5546, both from Bed 7 locality 1, Umzamba Estuary, Pondoland, Transkei, Umzamba Formation, Upper Santonian.

#### *Description and discussion*

Parts of two whorls, probably belonging to the same individual, are of special interest in that they agree with the general ornament of *P. stangeri* in all respects, apart from the fact that the venter is definitely tricarinate. On the smaller specimen, SAM-5687, the venter is preserved partially as an internal cast, and partially with the shell preserved (Fig. 93C). In both examples the lateral keels are continuous. On the larger fragment, SAM-K5546, which is part of a body chamber, the dorsum bears a distinct tricarinate impression of the previous whorl. The venter, unfortunately, is badly damaged and deformed. Part of a lateral keel is preserved at the proximal end, but this shows an undulation which may possibly be interpreted as a wavy lateral keel.

The present material is insufficient for erection of a new species, if it is, indeed, a representative of *Reginaites*.

The specimen occurs in the same horizon as that of *P. stangeri* in Pondoland, thus it does not seem possible to derive the species directly from *P. stangeri*. In this connection, however, it should be borne in mind that *P. stangeri* already occurs as early as Mid-Santonian in Madagascar (Collignon 1966a: 62, pl. 479 (fig. 1951)) and Lower Santonian of the Gulf Coast Cretaceous (Young 1963). It is interesting to note that the specimen figured by Collignon (1966a: 62, pl. 479 (fig. 1951)) has very elongated external tubercles, from which the present specimen may be derived.

Ornament of the present specimen is not compatible with that of the other known southern African species of *Reginaites*, or with *P. matsumotoi*, from which the latter are supposedly derived. If the specimen is, indeed, a true representative of *Reginaites*, it would seem to suggest that *Reginaites* is represented by two distinct, apparently independent lineages in southern Africa (Fig. 266).

#### *Occurrence*

Upper Santonian of Pondoland, Transkei.

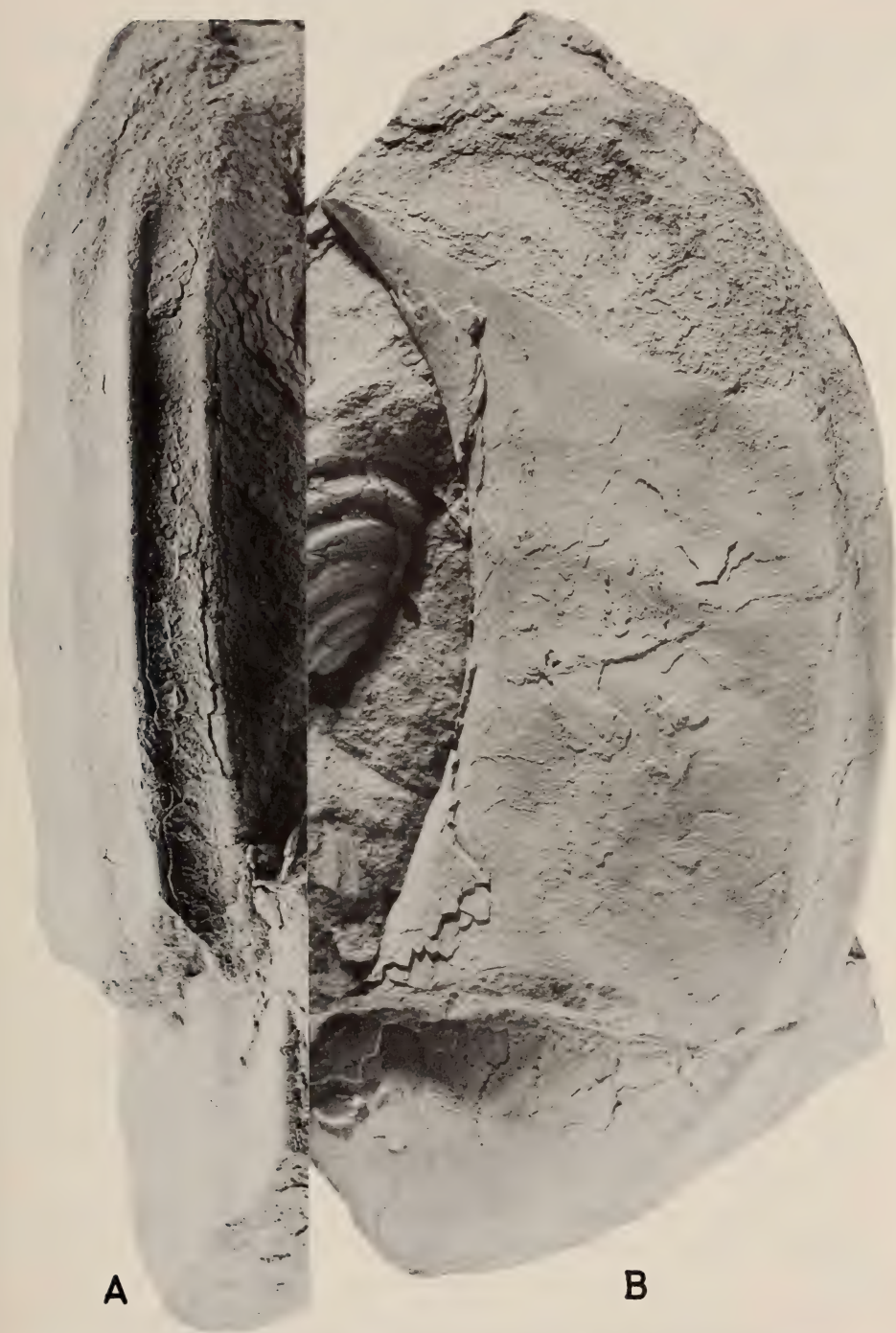


Fig. 94. *Reginaites zulu* sp. nov. Paratype SAS-H126A/4. Part of the body chamber.  $\times 0,8$ .

Genus *Texanites* Spath, 1932*Type species*

*Ammonites texanus* Roemer, 1852, by the original designation of Spath (1932: 379 footnote).

*Diagnosis*

Size of shell variable; may grow to enormous size. Coiling evolute to involute. Ornament consists from a relatively early stage of five rows of tubercles, with the lateral (2) row appearing last in ontogeny. Ornament is generally variable.

*Discussion*

In terms of numbers, the genus *Texanites* is the most important texanite taxon in the Upper Cretaceous deposits of southern Africa. Specimens referred to this genus display a bewildering array of intraspecific variation, which causes one to cast serious doubt on current texanitid systematics.

In his review of the genus, Matsumoto (1970: 270) listed the following species definitely referable to *Texanites*:

*Texanites dichotomus* Collignon (1948: 80, pl. 9(3) (fig. 3-3b), pl. 11(5) (fig. 1-1b)) from the Upper Santonian of Madagascar.

*Texanites gallicus* Collignon (1948: 75, pl. 8(2) (fig. 1-1a), text-fig. 9) from the Santonian of Madagascar, South America, and Europe.

*Texanites hispanicus* Collignon (1948: 76, pl. 8(2) (fig. 2-2b), text-fig. 11-11a) from the Santonian of Spain and Madagascar.

*Texanites hourcqi* Collignon (1948: 78, pl. 7(1) (fig. 1-1b), pl. 10(4) (fig. 1-1a)) from the Middle Santonian of Madagascar.

*Texanites interpositus* Collignon (1948: 82, pl. 7(1) (fig. 3), pl. 11(5) (fig. 2)) from the Upper Santonian of Madagascar.

*Texanites pseudotexanus* (de Grossouvre) (1894: 84) from the Santonian of Germany and Bohemia.

*Texanites quinquenodosus* (Redtenbacher) (1873: 108, pl. 24 (fig. 3a-b)) from the Santonian of Austria, France, Madagascar, and Angola, and tentatively from Hokkaido.

*Texanites roemeri* (Yabe & Shimizu) (1923: 2) from the Santonian of Texas.

*Texanites texanus* (Roemer) (1852: 31, pl. 3 (fig. 1a-c) *non* fig. 1e-d = *T. roemeri* Yabe & Shimizu) from the Santonian of North America and north Africa.

*Texanites venustus* Collignon (1948: 81, pl. 9(3) (fig. 4-4b)) from the Upper Santonian of Madagascar.

In addition to these definite contenders, a number of species based on incomplete material, generally lacking the inner whorls, were referred to the genus:

*Texanites americanus* (Lasswitz) (1904: 32, pl. 8 (fig. 1)) from the Lower to Middle Santonian of the Gulf Coast.



*Texanites lonsdalei* Young (1963: 90, pl. 34 (fig. 1), pl. 51 (figs 3–7), pl. 58 (figs 5–6), text-fig. 22a–d) from the Lower Campanian of Texas and Madagascar.

*Texanites mikobokensis* Collignon (1966a: 122, pl. 507 (fig. 2019), pl. 519 (fig. 2019)) from the Upper Santonian of Madagascar.

*Texanites oliveti* (Blanckenhorn) (1905: 104) from the Santonian of the Middle East.

*Texanites quadrangulatus* Collignon (1966a: 76, pl. 486 (fig. 1961)) from the Upper Santonian of Madagascar.

*Texanites rarecostus* Collignon (1966a: 78, pl. 487 (fig. 1965)) from the Middle Santonian of Madagascar.

To this list of doubtful contenders may be added:

*Texanites angolanus* Haas (1942: 12, figs 8–10, 11) from the Santonian of Angola.

*Texanites omeraense* (Reeside) (1927: 38, pl. 42 (figs 3–4), pl. 43 (figs 1–2)) from the Santonian of the Western Interior of North America.

*Texanites ralijaonai* Collignon (1966a: 130, pl. 511 (fig. 2023)) from the Santonian of Madagascar.

New species from South Africa, described below are:

*Texanites collignoni* sp. nov.

*Texanites postvanhoepeni* sp. nov.

*Texanites presoutoni* sp. nov.

*Texanites umzambiense* sp. nov.

*Texanites vanhoepeni* sp. nov.

In addition to displaying tremendous intraspecific variation, the Zululand *Texanites* species connect with *Paratexanites* and *Submortonicerias*.

*Texanites collignoni* may be derived from *Plesiotexanites collignoniforme* sp. nov., which in turn has its origin in *Paratexanites*. *Texanites soutoni* is derived, probably through *T. presoutoni* sp. nov., from *T. umzambiense* sp. nov., which is closely allied to, though apparently slightly younger than, *Plesiotexanites collignoniforme* sp. nov. *Texanites quadrangulatus* and *T. rarecostus* appear to connect with *Paratexanites*, without passing through a *Plesiotexanites* stage, via *Texanites vanhoepeni* sp. nov., the latter probably derived from *Paratexanites umkwelanensis*.

*Texanites soutoni* gradually gives rise to *Submortonicerias* towards the Santonian/Campanian boundary, and *Texanites vanhoepeni* and *T. postvanhoepeni* also show a distinct tendency towards acquisition of *Submortonicerias* characteristics in stratigraphically younger strata. This takes place through a gradual decrease in umbilical width and loss of lateral ornament. Details are given in the descriptions of the species. Similar trends are shown by *Texanites shiloensis* and *Submortonicerias tequesquitense* from the Gulf Coast of North America, which may possibly represent a geographically separated relative of the species group of *Texanites soutoni* and *Submortonicerias woodsi*.

The latter species group also shows what appears to be a distinct geographic differentiation into two groups inhabiting the deep and shallow waters of the St Lucia Formation and Umzamba Formation respectively.

*Texanites* is distinguished from *Plesiotesanites* by virtue of the early development of the pentatuberculate stage, although, in cases such as *T. umzambiense* sp. nov. and *P. collignoniforme* sp. nov., the distinction between the two taxa becomes subjective. None the less, *Plesiotesanites* should be maintained separate from *Texanites* as a distinctive group which provides the source for *Reginaites* and, in some cases, *Texanites*.

In large phragmocone or body chamber fragments it is impossible to distinguish between *Texanites* and *Plesiotesanites*, unless the ventrolateral tubercles are approximated in *Paratesanites* fashion.

As mentioned above, differences between *Texanites* and *Submortonicerias* are gradual, hence allocation of border-line cases such as *T. soutoni* to either of the genera becomes a matter of opinion, depending on where to draw the line between *Texanites* and *Submortonicerias*.

***Texanites collignoni* sp. nov.**

Figs 95, 96A, 97–98, 99B–C, 100–101

*Texanites oliveti* non Blanckenhorn: Collignon, 1948: 72, pl. 8(2) (figs 3–5), text-figs 5–8.

*Texanites oliveti* non Blanckenhorn var. *spinosa* Collignon, 1966a: 68, pl. 482 (fig. 1955).

?*Texanites oliveti* (Blanckenhorn): Matsumoto & Ueda 1962: 169, pl. 26 (fig. 2), text-fig. 13.

***Holotype***

SAM-PCZ5920 (Fig. 98), locality 74, north-western part of Die Rooiwal, Zululand, St Lucia Formation, Santonian I–II.

***Etymology***

Named after the late General Maurice Collignon, Moirans, France.

***Material***

Paratypes are SAS-H179/19, locality 6, excavations in the Enseleni Reserve, Zululand, St Lucia Formation, Santonian II–III; SAS-Z866, Z1754, Z1755, BMNH-C81551–C81558, locality 74, north-western part of False Bay at Die Rooiwal, Zululand, St Lucia Formation, Santonian I–II; SAS-Z351, from an unknown locality near Mfolozi, probably locality 14, St Lucia Formation, Santonian II to Campanian I; BMNH-C81507–C81508, from foreshore exposures west of Lister's Point, Zululand, St Lucia Formation, Santonian I–II; BMNH-C81515, from foreshore exposures north of Picnic Point, St Lucia Formation, Santonian I–II; a body chamber fragment NMB-D1353, locality 73, St Lucia Formation, Santonian I, may also be referred to this species; SAM-PCZ5711, labelled 'S.A. Cretaceous' also belongs to the species, and, judging by the matrix, this specimen may have been collected in the vicinity of locality 74 at Die Rooiwal.



Fig. 95. *Texanites collignoni* sp. nov. A. Suture line of paratype SAS-Z1755. Scale bar for suture in millimetres. B. Whorl section of paratype SAS-Z1754.  $\times 1$ .



*Dimensions*

|         | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|---------|----------|------------|------------|----------------|-------------|-------------|-------------|
| H179/19 | —        | 31,6       | 43,0       | 0,73           |             |             |             |
| Z866    | 255,0    | 66,0(29,3) | 86,0(33,7) | 0,77           | 116,0(45,5) | 32          | 32          |
| Z1754   | 257,0    | 59,0(22,9) | 89,0(34,6) | 0,66           | 117,0(45,5) | 27          | 33          |
| Z351    | 213,0    | 51,0(23,9) | 66,0(30,9) | 0,77           | 106,0(49,8) | 32          | 32          |
| Z1755   | 230,0    | 56,5(24,6) | 79,0(34,3) | 0,72           | 99,0(43,0)  | —           | —           |

*Description*

Coiling is evolute, with an umbilical width varying between 43 and 49 per cent of the diameter, but usually of the order of 45 per cent. Whorl overlap is minimal, and the dorsal zone of impression consequently small.

The whorl section in all the available specimens is higher than wide throughout, but differs in details from one specimen to another, and also throughout ontogeny (Fig. 95B, 96A). The umbilical wall is virtually vertical on the inner whorls, but becomes rounded on the outer whorls, merging gently into the gently inflated flanks. The flanks converge gradually to a rounded venter, narrower than the dorsum. In intercostal section maximum width is towards

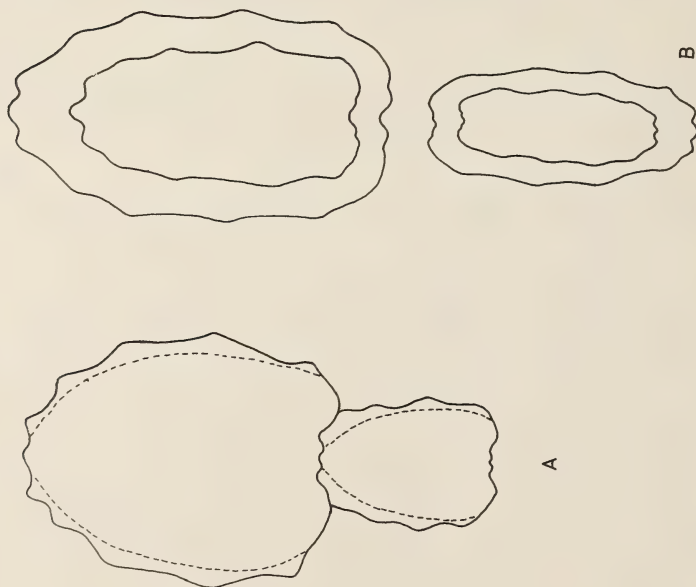


Fig. 96. A. *Texanites collignoni* sp. nov. Whorl section of paratype SAS-Z1755. B. Uncorrected sketches of whorl section of *Texanites oliveti* (Blanckenhorn, 1905) from Israel.  $\times 0,5$ .

the dorsal third of the flanks, coinciding with the position of the lateral tubercle.

None of the specimens has the innermost whorls preserved, and the earliest whorls preserved already show pentatuberculate ornament.

Typical ornament, as shown by SAS-Z866 (Fig. 97) and SAM-PCZ5920 (Fig. 98), consists of radial to slightly rursiradiate single ribs, each bearing a rounded to radially elongated umbilical (1) tubercle, displaced slightly ventrally

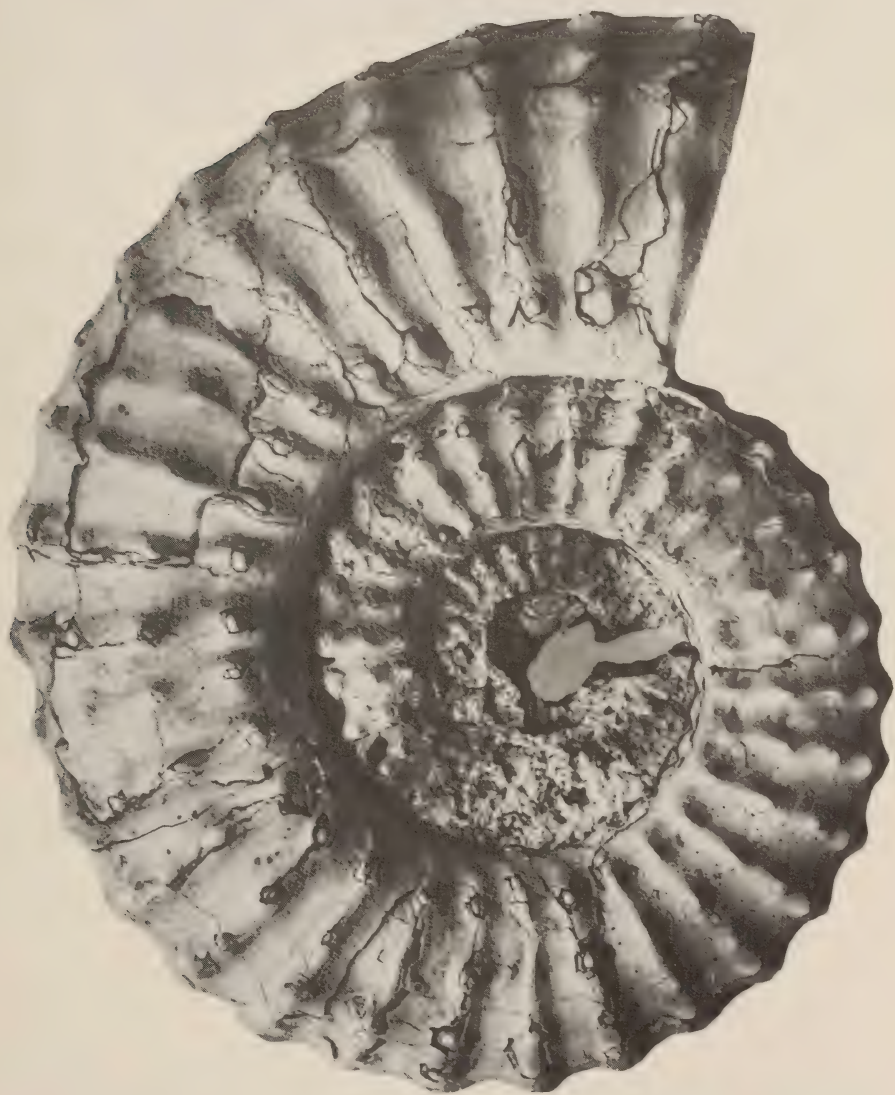


Fig. 97. *Texanites collignoni* sp. nov. Paratype SAS-Z866.  $\times 0,58$ .

from the umbilical edge, a prominent radially elongated, lateral (2) tubercle towards the dorsal third of the flanks (this tubercle juts out furthest laterally though it is not necessarily strongest developed), and progressively clavate submarginal (3), marginal (4) and external (5) tubercles over the rest of the flanks. With increasing diameter, and especially towards the body chamber, the umbilical and the lateral tubercles move ventrally, so that the former is some distance from the umbilical region and the latter nearer midflank. In typical forms ribbing is single, but some specimens feature bifurcations. The keel is undulating; undulations coinciding with lateral ornament.

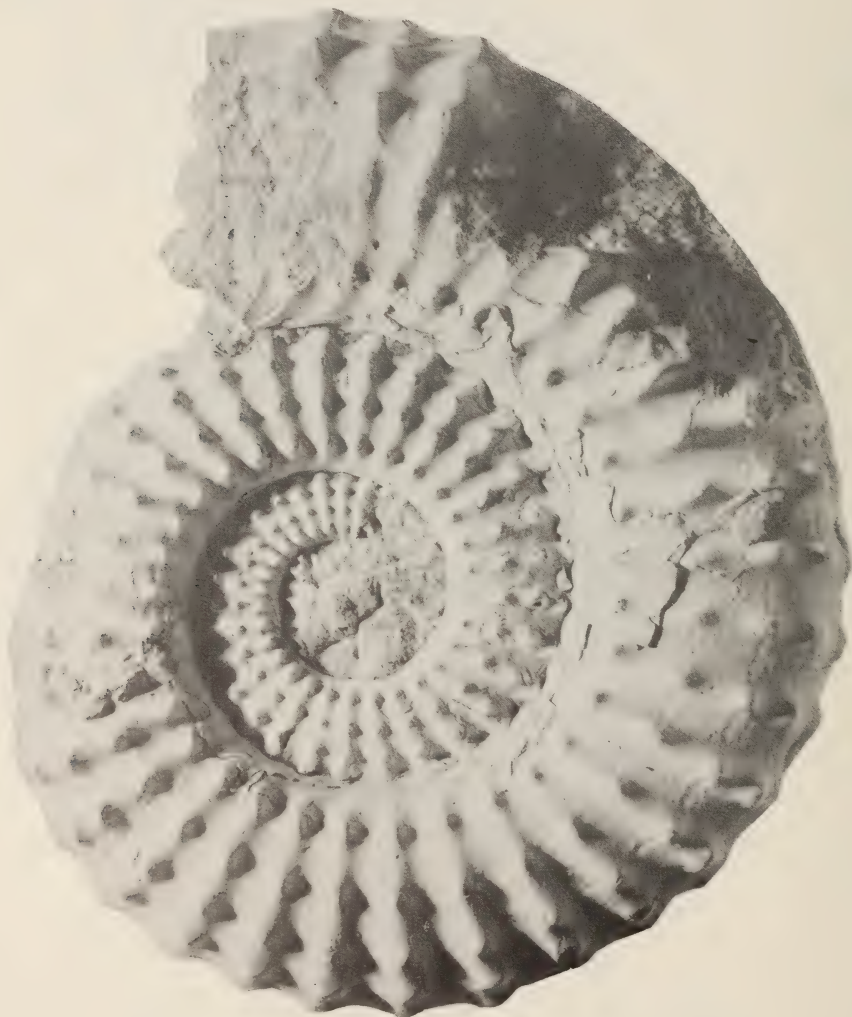


Fig. 98. *Texanites collignoni* sp. nov. Holotype SAM-PCZ5920.  $\times 0,5$ .



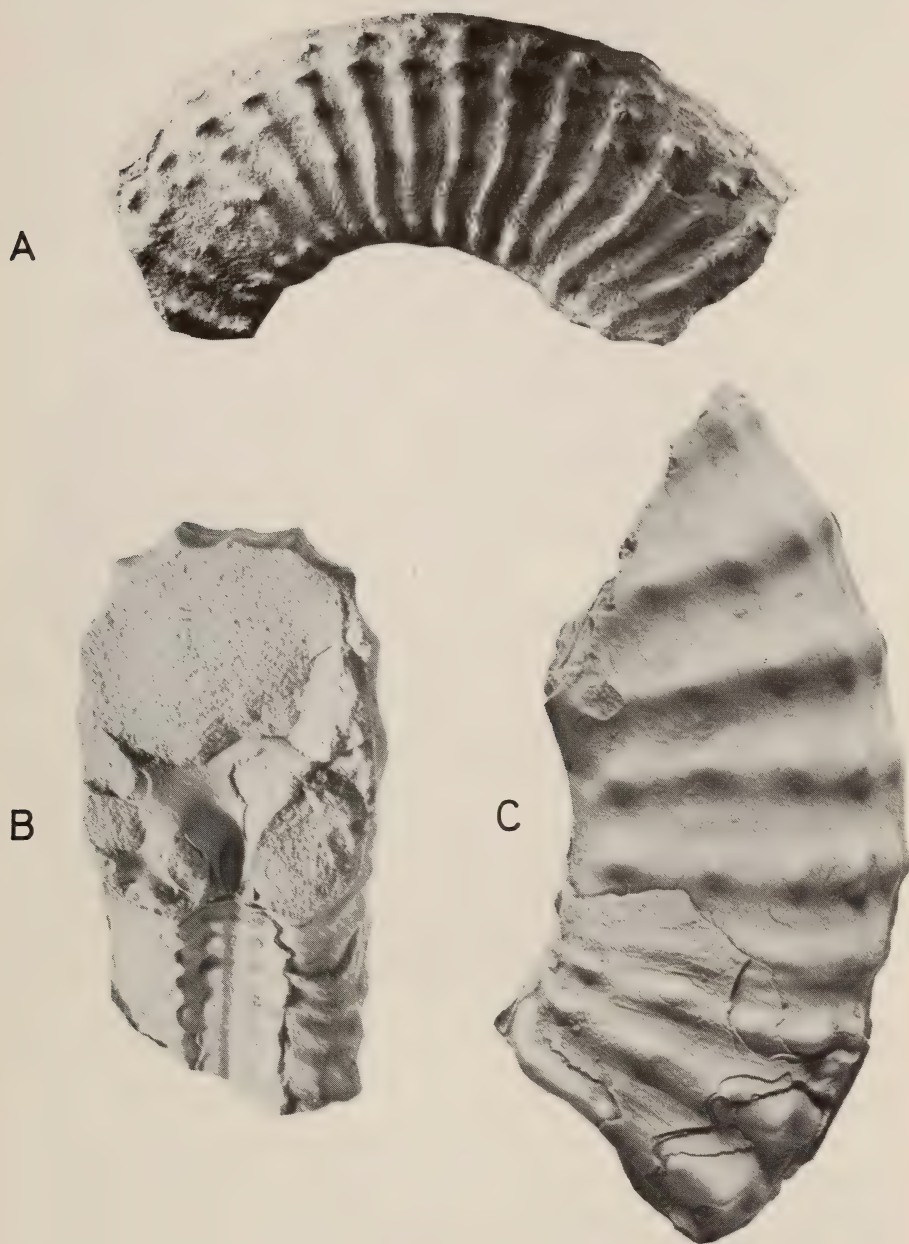


Fig. 99. A. *Texanites oliveti* (Blanckenhorn, 1905). Specimen from Judean desert. (Photograph Z. Lewy.) B-C. *Texanites collignoni* sp. nov. Paratype SAS-H179/19. This specimen remains rectangular to a large diameter.  $\times 1$ .



Fig. 100. *Texanites collignoni* sp. nov. Paratype SAS-Z1754.  $\times 0,5$ .

### Discussion

This species is common in the Lower Santonian of Zululand, and the authors (Kennedy & Klinger 1975: 279) initially identified it with *Texanites oliveti* (Blanckenhorn). *Texanites oliveti*, however, is a very poorly known species, as the figures provided by Taubenhaus (1920: 30, pl. 5 (figs 3, 5)) are very much reduced. According to Blanckenhorn (1905: 104) the species is identified by: 26 to 28 strong ribs, slightly narrower than the interspaces, simple, single, radial and slightly forwardly curved on the ventral third of the

flanks. The undulations on the keel correspond with the ribs. The ribs bear five rows of tubercles. . . . The umbilical tubercles and the two outer rows are strongest developed, while the second (lateral) row is always poorest developed. (Authors' free translation.)

This description fits the material rather well, but Z. Lewy (pers. comm. 1979) has informed the authors that, according to material from Israel, *T. oliveti* is a typically compressed form, with Wb : Wh ratio being of the order of 0,4 to 0,5 and seems to occur in the Upper Santonian only. A typical specimen from the Judean desert is here figured as Figure 99A, and whorl sections of other Israeli material as Figure 96B. Apart from the fact, thus, that the Zululand and Malagasy specimens are older than typical *T. oliveti*, they are also much more inflated, with Wb : Wh ratios of the order of 0,7. It seems advisable to refer the Zululand and Malagasy material to a new species, *T. collignoni* sp. nov., to separate it from the younger, more compressed *T. oliveti*. The specimen from the Lower Santonian of the Himenoura Group described by Matsumoto & Ueda (1962: 170) as *Texanites oliveti* (Blanckenhorn) also probably belongs to this species.

Collignon (1948: 72–75) discussed *T. collignoni* (as *T. oliveti*) at length, although his material consisted of small fragments only. Apart from the typical form, which has a more or less rectangular section, Collignon recognized two other varieties, var. *spinosa* and var. *triangularis*. Var. *spinosa* has more or less the same whorl section as the typical form, but differs in that the tubercles of the first three rows are rounded, and so strong that the intertubercular areas are as deep as the intercostal spaces. In var. *triangularis* the ornament is essentially the same as in the typical form, but the section is triangular.

As far as tuberculation is concerned, the Zululand material compares well with Collignon's descriptions and figures of the Malagasy material; as far as whorl section is concerned, the Zululand specimens are somewhat different in having a steeper or more rounded umbilical wall. The more complete Zululand specimens show that whorl section changes during growth, starting with rectangular section on the inner whorls, eventually becoming subrectangular to ovoid on the later parts of the phragmocone and body chamber. One of the specimens, however, SAS-H179/19 (Fig. 99B) retains the rectangular whorl section to a greater diameter than the other specimens.

In most of the specimens ribbing is single on the outer whorls. In SAS-Z1754 (Fig. 100), however, bifurcations are quite common on the outer whorls. Apart from being more compressed than the other specimens, there seems to be no other significant difference, and the specimen is also referred to *T. collignoni* sp. nov. It appears to connect morphologically with *T. soutoni*, described below.

Differences between *T. collignoni* and *T. texanus* are distinct in density of ribbing in typical forms, but become obscure when comparing *T. collignoni* with *T. texanus* var. *hispanica*. Here crenulation of the keel may be of assistance in differentiating between the species.

*T. quinquenodosus* (Figs 102–103) is a species with similar ribbing and coiling, but differs in that tuberculation is generally clavate in all the rows.



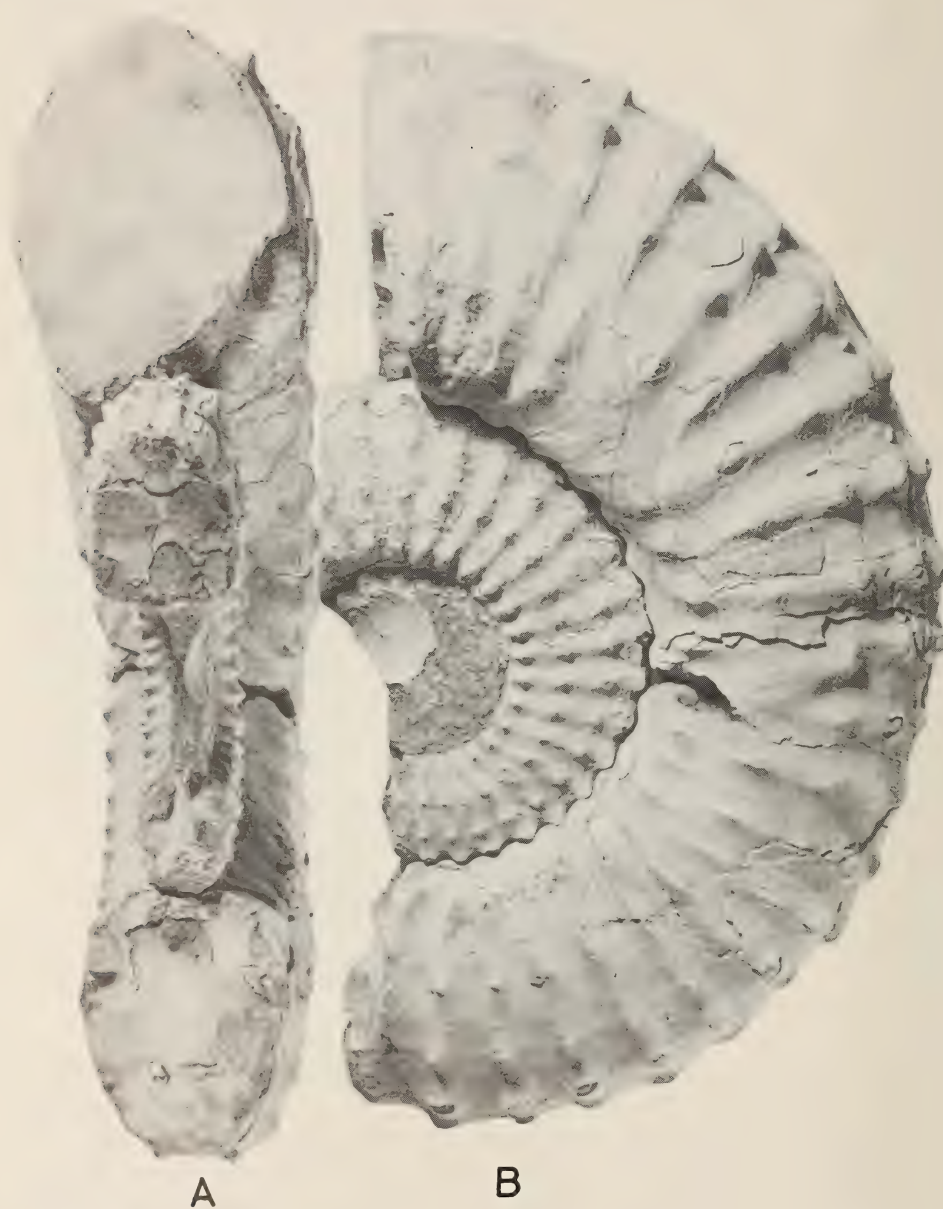


Fig. 101. *Texanites collignoni* sp. nov. Paratype SAS-Z1755.  $\times 0,6$ .

Even though all Redtenbacher's (1873) specimens were crushed, it appears as though the whorl section is more compressed than in *T. collignoni*. This raises the possibility that *T. oliveti* may be a junior synonym of *T. quinquenodosus*.

The rounded umbilical wall, ventrally displaced umbilical tubercle, and undulating keel in *T. collignoni* are very similar to *Plesiotexanites collignoniforme* sp. nov. described above (p. 89), and it seems reasonable to derive *T. collignoni* from that species.

*Schloenbachia* (*Mortoniceras*) *sandreckii* Blanckenhorn (1905: 105) may be allied, but is difficult to interpret. In this species only the external row of tubercles is developed, and it seems closer to *Submortoniceras* than *Texanites*.

*Schloenbachia* (*Mortoniceras*) *safedensis* Blanckenhorn (1905: 106) is another enigmatic species and may possibly represent a compressed specimen of *T. oliveti* or a closely allied species.

### Occurrence

Lower and Middle Santonian of Madagascar, Santonian I-II of Zululand, Lower Santonian of Japan.

[While this article was in press, a publication by Matsumoto & Haraguchi (Matsumoto, T. & Haraguchi, Y. 1978. A new Texanite Ammonite from Hokkaido. *Trans. Proc. Palaeont. Soc. Japan, N.S.* 110: 306-318) which has bearing on the discussion of *Texanites oliveti*, came to the notice of the authors. Matsumoto & Haraguchi suggest that *Texanites oliveti* is a good index species for the Lower Santonian, but also express doubt whether the specimens described by Collignon from Madagascar are, indeed, conspecific with the Middle East specimens of *T. oliveti*, and whether the latter is distinguishable from *T. quinquenodosus*. In view of our current knowledge and interpretation of *Texanites oliveti*, it is not a suitable index species for the Lower Santonian.

Pop & Szasz (Pop, G. & Szasz, L. 1973. Santonianul din Reguinea Hategului (Carpatii meridionali). *St. cerc. geol., geofiz., geogr., Ser. geologie* 18: 463-467) also described and figured a specimen as *Texanites oliveti* from Bulgaria, which seems identifiable with *T. collignoni*.]

### *Texanites quinquenodosus* (Redtenbacher, 1873)

Figs 102-103

*Ammonites texanus* Roemer: von Hauer, 1858: 10, pl. 2 (figs 4-6).

*Ammonites quinquenodosus* Redtenbacher, 1873: 108(18), pl. 24 (fig. 3a-b).

*Mortoniceras texanus* (Roemer): Zürcher, 1903: 686.

*Mortoniceras quinquenodosus* (Redtenbacher): Yabe & Shimizu, 1923: 30.

*Texanites quinquenodosus* (Redtenbacher): Collignon, 1948: 69(24), text-fig. 2; 1966a: 128, pl. 510 (fig. 2021). Matsumoto 1970: 272. Thomel, 1969: 12(120).

### Discussion

A full review of this species, based on all the original type material, is in preparation by the authors. One of the syntypes, now housed in the



Fig. 102. *Texanites quinquenodosus* (Redtenbacher, 1873). Plaster cast of one of Redtenbacher's syntypes from the Oberösterreichisches Landesmuseum, Linz.  $\times 0,65$ .





Fig. 103. *Texanites quinquenodosus* (Redtenbacher, 1873). Plaster cast of one of Redtenbacher's syntypes from the Oberösterreichisches Landesmuseum, Linz.  $\times 0,65$ .

Oberösterreichisches Landesmuseum, Linz (Austria), is here figured photographically (Figs 102–103) for comparison with the South African material.

*Texanites quadrangulatus* Collignon, 1966

Figs 104–108

*Texanites quadrangulatus* Collignon, 1966a: 76, pl. 486 (fig. 1961).

*Holotype*

The specimen figured by Collignon (1966a, pl. 486 (fig. 1961)) from the Upper Santonian of Madagascar, Zone of *Pseudoschloenbachia umbulazi*.

*Material*

SAS-A2580, SAS-Z1760, SAM-PCZ5879–PCZ5882, BMNH-C81513–C81514, all from locality 74, False Bay, Zululand, St Lucia Formation, Santonian I to Campanian I; SAS-H179/18, locality 6, Enseleni Reserve, Zululand, St Lucia Formation, Santonian II to Campanian I; SAS-Z595, locality 14, Mfolozi, Zululand, St Lucia Formation, Santonian II–III; BMNH-C81511, locality 84, False Bay, St Lucia Formation, Santonian I.

*Dimensions*

|   | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|---|----------|------------|------------|----------------|------------|-------------|-------------|
| H179/18                                     | —        | 27,0       | 27,0       | 1,0            | —          | —           | —           |
| PCZ5879                                     | 125,0    | 48,0(38,4) | 51,0(40,8) | 0,94           | 46,0(36,8) | 11 × 2      | —           |
| PCZ5880                                     | 142,0    | 54,0(38,0) | 54,0(38,0) | 1,0            | 58,0(40,8) | 25          | 26          |
| Z1760                                       | 175,0    | 65,0(37,1) | 71,0(40,6) | 0,91           | 61,0(34,9) | 13 × 2      | —           |
| A2580                                       | 245,0    | 76,0(31,0) | 93,0(38,0) | 0,82           | 93,0(38,0) | 29          | 29          |
| Holotype<br>after<br>Collignon<br>1966a: 76 | 145,0    | 50,0(34,0) | 50,0(34,0) | 1,0            | 59,0(41,0) | —           | ? 30        |

*Description*

Coiling is relatively evolute, with an umbilical diameter of 35 to 41 per cent of the total diameter. Whorl overlap is minimal with the marginal (4) tubercles clearly exposed in the umbilical seam. Increase in diameter is rapid.

The costal whorl section on the phragmocone is distinctly quadrate, sometimes even wider than high in early stages, whereas the intercostal section is more rounded (Figs 106B, 108). Towards the later part of the phragmocone the whorl section becomes more rounded (Fig. 107B), higher than wide, and eventually dome-shaped on the body chamber (Fig. 105A). Ornament on the phragmocone consists of prominent ribs bearing very strong tubercles and separated by wider interspaces. The umbilical (1) tubercles are conical to radially elongated, pointed slightly inwards and with bases extending a little distance down the umbilical wall. The lateral (2) tubercles are situated at midflank or on the dorsal third of the flanks and are conical to clavate, and separated from the umbilical tubercles by a depression on the ribs. The sub-marginal (3), marginal (4), and external (5) tubercles are situated closer to each



Fig. 104. *Texanites quadrangulatus* Collignon, 1966. SAS-A2580.  $\times 0,58$ .

other than the umbilical and lateral ones throughout ontogeny, but especially on the inner whorls. Here the submarginal tubercles may be tremendously enlarged and partially fused to the marginal tubercles, having the appearance of *Paratexanites*. The external (5) tubercles are very clavate and generally as high as, or higher than, the central keel. Bifurcations occur, but not frequently. Towards the later part of the phragmocone and the body chamber, all ornament becomes subdued (Fig. 104).





Fig. 105. *Texanites quadrangulatus* Collignon, 1966. SAS-A2580.  $\times 0,58$ .



Fig. 106. *Texanites quadrangulatus* Collignon, 1966. SAM-PCZ5881. Suture line,  $\times 5$ . Whorl section,  $\times 1$ .

The external suture comprises a blocky, wide E/L saddle, narrow L/U2 saddle and long, narrow lateral lobe (L), somewhat restricted towards the top (Fig. 106A).

#### Discussion

The quadrate whorl section on the greater part of the phragmocone, strong ornament and, depending on preservation, strong development of the submarginal tubercle and *Paratexanites*-like spacing of the submarginal (3),



Fig. 107. *Texanites quadrangulatus* Collignon, 1966. SAM-PCZ5879.  $\times 1$ .



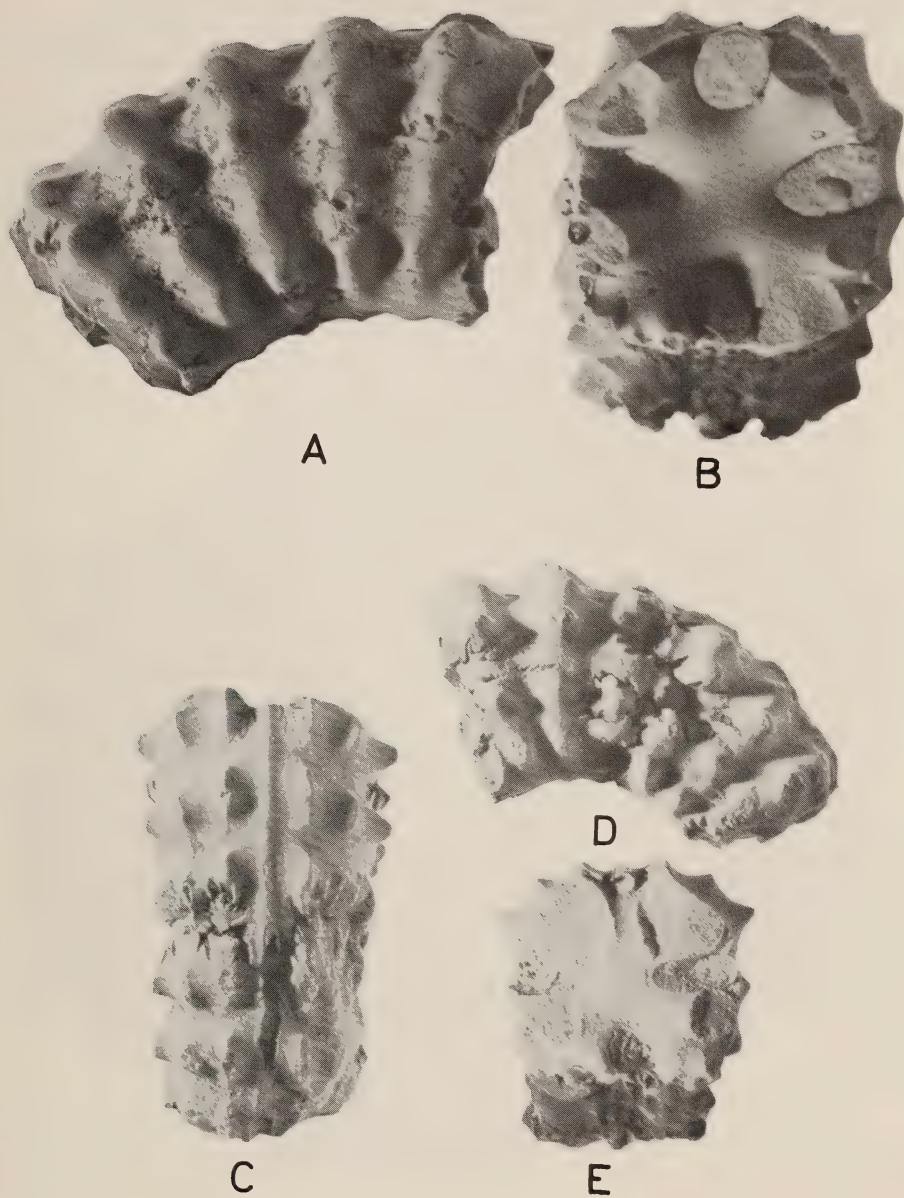


Fig. 108. *Texanites quadrangulatus* Collignon, 1966. A-B. SAM-PCZ5881.  
C-E. SAS-H179/18.  $\times 1$ .

marginal (4), and external (5) tubercles are all characteristic of the species.

*T. vanhoepeni* is a similar, though older, species. Here, however, the rate of increase of diameter is greater than in *T. quadrangulatus*, the whorl section is more rounded in the adult stage, and it lacks the strong ornament.

Matsumoto (1970: 272) speculated on the origin of *T. quadrangulatus*, suggesting that it could be derived from *Protexanites bourgeoisi* or *Paratexanites serratomarginatus grossouvrei*.

Present material suggests that it would seem more feasible to derive *T. quadrangulatus* from *Paratexanites pseudotricarinatum* or *P. umkwelanense*, possibly via *T. vanhoepeni*.

#### Occurrence

Middle and Upper Santonian of Madagascar and Zululand.

#### *Texanites vanhoepeni* sp. nov.

Figs 109–117

#### Holotype

SAS-Z879 (Figs 109–110), locality 83, foreshore exposures at Mason's Camp, south-western part of False Bay, Zululand, St Lucia Formation, Coniacian IV.

#### Etymology

Named for the late Dr E. C. N. van Hoepen.

#### Material

Paratypes are SAS-Z1792, Z2110, H201/33, and BMNH-C81534–C81535, locality 84, beach exposures in the south-western part of False Bay, Zululand, St Lucia Formation, Santonian I; BMNH-C81509–C81510, C81521, C81537, locality 85, Santonian I; SAS-H200/92 from the same horizon and locality as the holotype; NMB-D1364 and D1379, from the same region at locality 86, St Lucia Formation, Coniacian V to Santonian I or II; NMB-D1353, locality 73, the lower reaches of the Mzinene River, St Lucia Formation, Coniacian to Santonian; and BMNH-C81559, locality 74, St Lucia Formation, Santonian I–II.

#### Dimensions

|         | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|---------|----------|------------|------------|----------------|------------|-------------|-------------|
| Z879    | 183,0    | 69,0(37,7) | 71,0(38,8) | 0,97           | 70,0(38,2) | 24          | 24          |
| H200/92 | 192,0    | —          | 67,0(34,9) | —              | 79,0(41,1) | 28          | 28          |

#### Description

Coiling is evolute, with rapidly increasing whorls (Figs 111–112). The whorl section is more or less equidimensional throughout, but changes from subquadrate to rounded during growth, especially at the umbilical edges (Fig. 113A).



Fig. 109. *Texanites vanhoepeni* sp. nov. Holotype, SAS-Z879.  $\times 0,86$ .





Fig. 110. *Texanites vanhoepeni* sp. nov. Holotype, SAS-Z879.  $\times 0,8$ .



Fig. 111. *Texanites vanhoepeni* sp. nov. Paratype SAS-H201/33.  $\times 1$ .

None of the specimens has the very innermost whorls preserved to show the ontogeny. Ornament on the phragmocone consists of sparse, single radial ribs bearing prominent tubercles. Rib density is generally of the order of 24, but may be as high as 28. The umbilical (1) tubercles are radially elongated, pointing slightly inwards. The lateral (2) tubercles at the dorsal third of the flanks are usually very prominent and conical to slightly clavate. The submarginal (3) at the ventral third of the flanks is clavate and generally smallest.



Fig. 112. *Texanites vanhoepeni* sp. nov. Paratype SAS-H201/33.  $\times 1$ .

The marginal (4) and external (5) tubercles are very clavate, and, in some cases, situated closer to each other than the submarginal (3) and marginal (4). These former tubercles may be strongly developed, and protrude far above the venter.

The keel is very low and poorly developed, but distinctly undulating, in some cases forming a row of weakly clavate tubercles along the siphonal line corresponding in location to the ribs.

The suture has a very long and thin lateral lobe (L) (Fig. 113B).





Fig. 113. *Texanites vanhoepeni* sp. nov. A. Whorl section of paratype SAS-H201/33. B. Partial suture line of paratype SAS-Z2111.  $\times 1$ .

On the body chamber ornament remains prominent, but becomes wider spaced (Figs 114–115).

#### *Discussion*

This species is easily distinguished by the rapid increase in whorl diameter, generally sparse costation and undulating keel.

Unfortunately, the available material of this species is limited, and accurate stratigraphic data scant. There does, however, seem to be a tendency towards



Fig. 114. *Texanites vanhoepeni* sp. nov. Paratype NMB-D1364. Specimen illustrating wider spacing of ornament towards and on body chamber.  $\times 0,5$ .



Fig. 115. *Texanites vanhoepeni* sp. nov. Paratype NMB-D1379. Body chamber fragment.  
× 0,66.



tighter coiling higher up in the sequence, giving rise to a *Submortonicer*-like form, *Texanites postvanhoepeni* sp. nov., described below. This tendency in coiling is illustrated by SAS-H200/92 (Fig. 116) with widest umbilical width at 41 per cent, through the holotype SAS-Z879 (Fig. 109) with umbilical width of 38 per cent, to SAS-Z2100 (Fig. 117) with an umbilical diameter of about 33 per cent.

The rounded whorl section in the adult stage, and the undulating keel relate this species to *Texanites collignoni*, *Plesiotexanites collignoniforme*, *Paratexanites umkwelanense* and *P. pseudotricarinatum*. Stratigraphic data seem to suggest that *T. vanhoepeni* may be derived from *P. umkwelanense*, or some common ancestral form. Apart from the lateral tubercle, the whorl section of the two species is remarkably alike, as is the prominence of the marginal (4) and external (5) tubercles in cases.

Unfortunately, the very innermost whorls are not preserved, but at a



Fig. 116. *Texanites vanhoepeni* sp. nov. Paratype SAS-H200/92. Specimen with greatest umbilical width.  $\times 0,55$ .



Fig. 117. *Texanites vanhoepeni* sp. nov. Paratype SAS-Z2110. Specimen with smallest umbilical width.  $\times 1$ .

diameter of 45 mm lateral tubercles are already present, indicating that this is probably a *Texanites* and not referable to *Plesiotexanites*. This suggests that in this case *Texanites* s.s. was derived directly from *Paratexanites* without a *Plesiotexanites* stage as in the case of *T. collignoni* (p. 126).

*Texanites collignoni* differs in having a completely different whorl section and much slower expanding whorls, as does *Plesiotexanites collignoniforme*.

As far as lateral ornament is concerned, there is close resemblance to *Texanites ralijaonai* from the Upper Santonian of Bevaho (Belo sur Tsiribihina), Madagascar. In that species, however, increase in whorl diameter is not as rapid as in the present species as Collignon's (1966a: pl. 512 (fig. 2023)) figure shows. That species also lacks an undulating keel.

*Texanites rarecostus* Collignon from Zululand and Madagascar has similar sparse costation, c. 23–24 per whorl, but has less massive whorls and a very slow rate of whorl increase.

*Texanites quadrangulatus* has proportions and ornament which overlaps with that of the present species to a certain extent, and it is possible that they are genetically related. *T. quadrangulatus*, however, generally has less massive whorls, a slower increase in diameter, a smaller lateral tubercle and has the three ventral rows approximated.

#### Occurrence

Upper Coniacian to Lower Santonian of Zululand.

#### *Texanites postvanhoepeni* sp. nov.

Figs 118–120

#### Holotype

SAM-PCZ5902 (Fig. 118), locality 85 or 86, foreshore exposures at Mason's Camp, south-western part of False Bay, Zululand, St Lucia Formation, Coniacian V to Santonian I and II.

#### Etymology

Refers to possible derivation from *Texanites vanhoepeni*.

#### Material

SAS-Z1787 and BMNH-C81522 from the same locality and horizon as the holotype.

#### Dimensions

|         | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb: Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|---------|----------|------------|------------|---------------|------------|-------------|-------------|
| PCZ5902 | 182,0    | 68,0(38,2) | 80,0(43,9) | 0,85          | 59,0(32,4) | 20          | 32          |
| Z1787   | 220,0    | 84,0(38,2) | 96,0(43,6) | 0,87          | 67,0(30,4) | —           | —           |

#### Description

Coiling is involute, with an umbilical width of 30 to 32 per cent, and very rapidly increasing whorls. The dorsal zone of impression, however, is very



shallow, and successive whorls cover each other only up to the middle of the marginal (4) tubercle.

The whorl section throughout, as far as visible, is higher than wide, with an overhanging to vertical umbilical wall, flanks parallel up to the lateral (2) tubercle, which marks the greatest width, and then converging slowly to the marginal (4) and eventually the external (5) tubercle (Fig. 120A).

On the innermost whorls preserved, ribs bifurcate quite frequently. Small,



Fig. 118. *Texanites postvanhoepeni* sp. nov. Holotype SAM-PCZ5902.  $\times 0,67$ .



Fig. 119. *Texanites postvanhoepeni* sp. nov. Paratype SAS-Z1787.  $\times 0,67$ .

conical umbilical (1), lateral (2), submarginal (3), and clavate marginal (4) tubercles are exposed on the flanks. Beyond a diameter of c. 70 mm, all lateral ornament weakens progressively, though never disappearing completely.

The suture is incompletely exposed, but shows a subtrifid, long and narrow lateral lobe (L).



Fig. 120. *Texanites postvanhoepeni* sp. nov. Paratype SAS-Z1787.  $\times 0,67$ .



### Discussion

As mentioned above (p. 152), this species appears to be the end member in a series of specimens with progressively tighter coiling. Starting with an evolute form of *T. vanhoepeni* sp. nov. with an umbilical diameter of 41 per cent, it terminates with the present species, with an umbilical width of only 30 to 32 per cent. Unfortunately precise stratigraphic data are lacking to fully confirm this assumption, but it would be in line with the general recoiling pattern observed in *T. soutoni* and allied species (described below, p. 172). As in the latter, the dividing line here between *Texanites* and *Submortonicerases* becomes arbitrary. Because the holotype still has weak lateral tubercles present at the largest diameter preserved, the species is referred to *Texanites* rather than *Submortonicerases*.

*Texanites quadrangulatus* has a very similar shape, but differs mainly in having a very prominent quadrate whorl section on the early part of the phragmocone, much stronger tuberculation and a slightly wider umbilicus (34–40%).

*T. postvanhoepeni* is similar to *Submortonicerases woodsii*, but in the latter the whorl section is more compressed, and coiling looser.

### Occurrence

Lower to Middle Santonian of Zululand.

### *Texanites rarecostus* Collignon, 1966

Figs 121–122

*Texanites rarecostus* Collignon, 1966a: 78, pl. 487 (fig. 1965).

### Type

Holotype by monotypy is the specimen figured by Collignon (1966a: pl. 487 (fig. 1965)) from the Middle Santonian of Beantaly-Souromaraino, Madagascar.

### Material

SAS-Z596, locality 14, Mfolozi, Zululand, St Lucia Formation Santonian II and III to Campanian I; and SAM-PCZ5878 from an unknown locality, presumably locality 74, the north-western end of False Bay, Zululand, St Lucia Formation, Santonian to Campanian.

### Dimensions

|                                | D    | Wb         | Wh         | Wb : Wh | U          | Int.   | Ext.   |
|--------------------------------|------|------------|------------|---------|------------|--------|--------|
| Z596                           | 120  | 31,0(25,8) | 34,0(28,3) | 0,91    | 59,0(49,2) | 13 × 2 | 13 × 2 |
|                                | 64,0 | 18,5(28,9) | 20,0(31,3) | 0,92    | 30,0(46,9) | 13 × 2 | 13 × 2 |
| PCZ5878                        | 102  | 30,0(29,4) | 33,0(32,4) | 0,91    | 50,0(49,0) | 11 × 2 | 11 × 2 |
| Holotype<br>after<br>Collignon | 128  | 38,0(30,0) | 40,0(31,0) | 0,95    | 62,0(48,0) | 23     | 24     |

*Description*

Two incomplete specimens with part of the body chamber preserved are tentatively referred to Collignon's species. Coiling is very evolute with an umbilical width of 46 to 49 per cent of the diameter. Whorl overlap is very small with the marginal tubercles clearly exposed in the umbilical suture.

The intercostal whorl section is rounded with maximum width at midflank



Fig. 121. *Texanites rarecostus* Collignon, 1966. SAS-Z596. A  $\times 1,05$ ; B  $\times 1,3$ .

or at the umbilical edge. Costal whorl section is subquadrangular, slightly higher than wide with maximum whorl breadth at the umbilical (1) tubercle or lateral (2) tubercle, but later migrating towards the submarginal (3) tubercle.

SAS-Z596 shows part of the early ontogeny. At a diameter of 14 mm ornament consists of regularly bifurcating thin ribs displaying conical umbilical (1) and submarginal (3) tubercles on the exposed flank. At a diameter of c. 32 mm ribs still bifurcate regularly, rib density being about 11 (bifurcating ribs) per half whorl. The submarginal (3) tubercles have now migrated towards the ventral quarter or third of the exposed flanks, exposing the marginal (4) tubercles in the umbilical suture. Lateral (2) tubercles start appearing at a diameter of c. 40 mm, and at this stage the four exposed rows are arranged equidistantly on the flanks. Bifurcations occur less frequently, and all ornament coarsens, resulting in a lower rib density.

In the adult stage the umbilical (1) and lateral (2) tubercles are distinctly conical, while the remaining three rows are clavate.

The keel is entire, and generally lower than the external tubercles. The suture has massive saddles and a U-shaped lateral lobe (L).

### Discussion

The holotype of the species consists of slightly more than a whorl and is difficult to interpret. The Zululand specimens have comparable relative proportions, but seem to have more robust ornament. In addition, SAS-Z596 has distinctly prorsiradiate ribs on the outer whorl compared to rectiradiate on the holotype. On the basis of the limited material available, it is not known whether these differences are of any significance.

Differences between *T. rarecostus* and *T. americanus* are not very clear. The outer whorl of SAS-Z596 (Fig. 121) is very similar to the holotype of *T. americanus* (see Lasswitz 1904, pl. 8 (fig. 1)). The inner whorls of the holotype, however, are not as densely costate as those of the Zululand specimen. Young (1963: 83-4) suggested that Lasswitz's artist may have erred in drawing the inner whorls of the holotype. Even Young's material, however, is more coarsely costate on the inner whorls (compare Young 1963: pl. 44 (fig. 2)). On the other hand, if density of ribbing on the inner whorls of *Plesiotexanites* is taken into consideration, this difference seems very trivial indeed. Of more importance seems to be the difference in whorl section, that of *T. americanus* being more inflated than that of *T. rarecostus*. For the present the two species are retained apart, in cognizance of their close resemblance.

*Plesiotexanites stangeri* is a similarly evolute species, but differs in the late development of the lateral tubercle and in generally lacking the strong ornament on the body chamber of *T. rarecostus*.

Small specimens of the inner whorls of *T. vanhoepeni* sp. nov. may be mistaken for *T. rarecostus* in having a similar whorl section, but in more complete material the rapid increase in size is apparent.

Another allied species is *T. quadrangulatus*, but in the latter the whorl





Fig. 122. *Texanites rarecostus* Collignon, 1966. SAM-PCZ5878.  $\times 1$ .

section is more quadrate at larger diameters, and increase in size is also much more rapid.

#### Occurrence

*T. rarecostus* occurs in the Middle Santonian of Madagascar, Zone of *Texanites hourcqi* and Santonian of Zululand.

#### *Texanites texanus* s.l. (Roemer, 1852)

Figs 123–125

*Texanites texanus* (Roemer): Collignon, 1948: 66(20), text-fig. 1–1b (with synonymy); 1966b: 52, pl. 33.

*Texanites texanus* var. *gallica* Collignon, 1948: 75(30), pl. 8(2), (fig. 1–1a), text-figs 9–10.

*Texanites texanus* var. *hispanica* Collignon, 1948: 76(31), pl. 8(2) (fig. 2–2b), text-fig. 11–11a.

*Texanites texanus texanus* (Roemer): Young, 1963: 80, pl. 38 (figs 1–2), pl. 40 (figs 1–3), pl. 41 (fig. 4), text-figs 21g, 22e, 25d.

*Texanites texanus gallica* Collignon: Young, 1963: 82, pl. 38 (figs 3–4).

*Texanites texanus twiningi* Young, 1963: 82, pl. 38 (fig. 5), pl. 39 (fig. 1), pl. 41 (figs 2, 5), pl. 48 (fig. 4).

*Texanites gallicus* Collignon, 1966a: 78, pl. 487 (fig. 1964).

*Texanites hispanicus* Collignon, 1966a: 128, pl. 510 (fig. 2022).

#### Material

SAS–H139, locality 14, road cuttings near Mfolozi, Zululand, St Lucia Formation, Santonian II–III to Campanian I; and an unnumbered specimen in the offices of the Geological Survey, Cape Town, here referred to as GSO CT, from an unspecified horizon at locality 1, Umzamba Cliff, Pondoland, Transkei, Umzamba Formation, Santonian to Campanian.

#### Dimensions

|                       | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|-----------------------|----------|------------|------------|----------------|-------------|-------------|-------------|
|                       |          |            |            |                |             | <i>I</i>    | <i>T</i>    |
| SAS–H139              | 165      | 44,5(27,0) | 57,0(34,5) | 0,78           | 72,7(44,1)  | 31          | 33          |
|                       | 114,2    | 32,8(28,7) | 39,8(34,8) | 0,82           | 48,3(42,3)  | 29          | 34          |
| GSO CT                | 223,9    | —          | 71,6(31,9) | —              | 101,5(45,3) | 36          | 36          |
| (unnumbered specimen) |          |            |            |                |             |             |             |

#### Description

SAS–H139 and GSO CT are fairly complete specimens with parts of the body chamber preserved. Coiling is evolute, with an umbilical diameter measuring 42 to 45 per cent of the total diameter. Whorl overlap is minimal, covering the successive whorls up to the marginal (4) tubercles. The whorl section throughout is higher than wide, with a sub-ovoid to subrectangular whorl section both in costal and intercostal section.

Specimen SAS–H139 has the innermost whorls preserved up to a diameter of 7 mm. Here ornament consists of regularly bifurcating ribs with weak umbilical, and strong ventrolateral, spines. Beyond a diameter of 7 mm ribs bifurcate frequently with occasional single ribs. The ventrolateral row of tubercles progressively migrates away from the umbilical wall to expose a

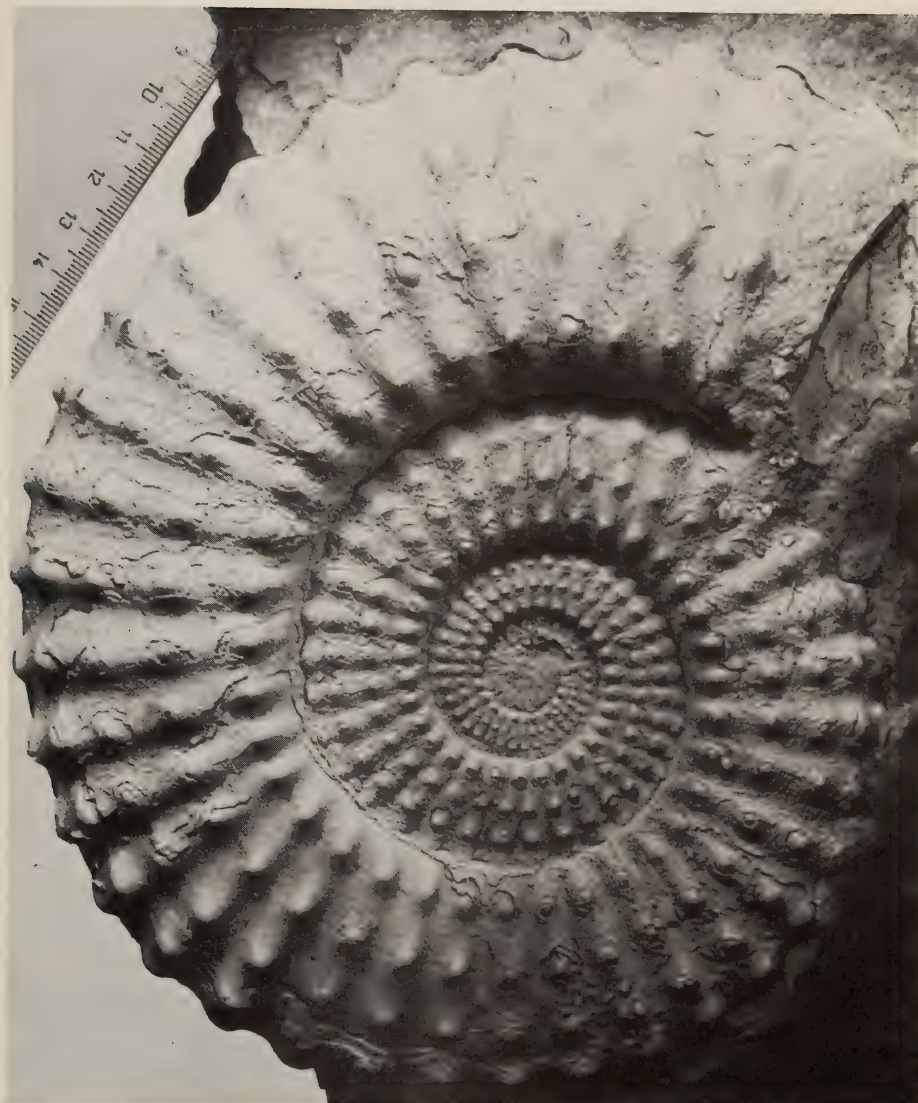


Fig. 123. *Texanites texanus* (Roemer, 1852). Unnumbered specimen from the Cape Town branch of the Geological Survey. Probably referable to subspecies or variety *hispanica*.





Fig. 124. *Texanites texanus* (Roemer, 1852). SAS-H139. This specimen is best referred to subspecies or variety *gallica*.  $\times 0,8$ .

third row of tubercles in the umbilical suture. Weak lateral (2) tubercles start appearing at a diameter of c. 20 mm near the dorsal third of the flanks. Beyond that diameter ornament remains more or less the same. The only significant change is that tuberculation becomes more prominent, and bifurcations less frequent, to eventually disappear completely on the body chamber.

The ribs are generally straight and slightly rursiradiate throughout. The umbilical (1) tubercles are conical to radially elongated, pointing slightly inwards. The lateral (2) tubercles are conical on the inner whorls, but become prominently elongated in the direction of the ribs in later whorls. The sub-marginal (3) tubercles are conical to radially elongated, whilst the marginal (4) and external (5) tubercles are clavate.

GSO CT differs from SAS-H139 in having the lateral tubercle situated virtually at midflank, compared to the dorsal third in the latter.

The keel is low and entire.

### Discussion

Collignon (1948) correctly interpreted *T. texanus* s.s. and removed all European references to this species from the strict synonymy. Apart from the typical form, he recognized two distinct varieties, var. *hispanica* and var. *gallica*, but later (1966a) elevated them to specific rank. Young (1963) added another, *T. texanus twiningi*, as a subspecies. Differences between the four subspecies or varieties are based mainly on density of ribbing and details of ornamentation. *T. texanus texanus* appears to have single ribs only, numbering about 20 to 21 per whorl. *T. texanus twiningi* has four to six more ribs per whorl than the nominate subspecies. *T. texanus gallica* has a sub-ovoid whorl section, and denser costation than the nominate subspecies, and the lateral tubercle is situated on the dorsal third of the flanks. *T. texanus hispanica* also has denser costation, but ribbing starts at the umbilical wall and the lateral tubercle migrates ventrally until it is finally situated at midflank.

*T. texanus* s.l. is not a very common species, hence it is difficult to decide whether the four varieties, subspecies or species really merit separation, or whether this is merely another example of morphological classification in the texanitids. If large collections were available, as in the case of *P. stangeri* or *T. soutoni*, these differences could possibly all be incorporated in the intra-specific variation of a single species. Young (1963: 82) separated *T. texanus twiningi* from the nominate subspecies purely on the grounds of stratigraphic separation, stating that 'if the two forms, *T. texanus texanus* and *T. texanus twiningi* occurred together, there would be no need for the new name'. There does, however, seem to be an age difference between the two subspecies, each being utilized to designate a biozone (Young 1963: 22, text-fig. 33).

Of the South African specimens, SAS-H139 is best referred to *T. texanus gallica*, having the lateral tubercle situated at the dorsal third of the flanks.

The Pondoland specimen GSO CT has the lateral tubercle situated at midflank on the body chamber, and may be referred to *T. texanus hispanica*. It should be pointed out, however, that it lacks the extension of ribbing on to the umbilical wall, alleged to be characteristic of *T. texanus hispanica*.

### Occurrence

*Texanites texanus texanus* appears to be restricted to Texas, although Peron (1897: 49-50) has also recorded the species from Mansourah in Algeria. Without figures the latter record is questionable. *T. texanus twiningi* is also restricted to Texas. *T. texanus gallica* has been recorded from France, Bulgaria, ?Italy, South America, Texas and Madagascar. *T. texanus hispanica* is known from Spain and Madagascar.

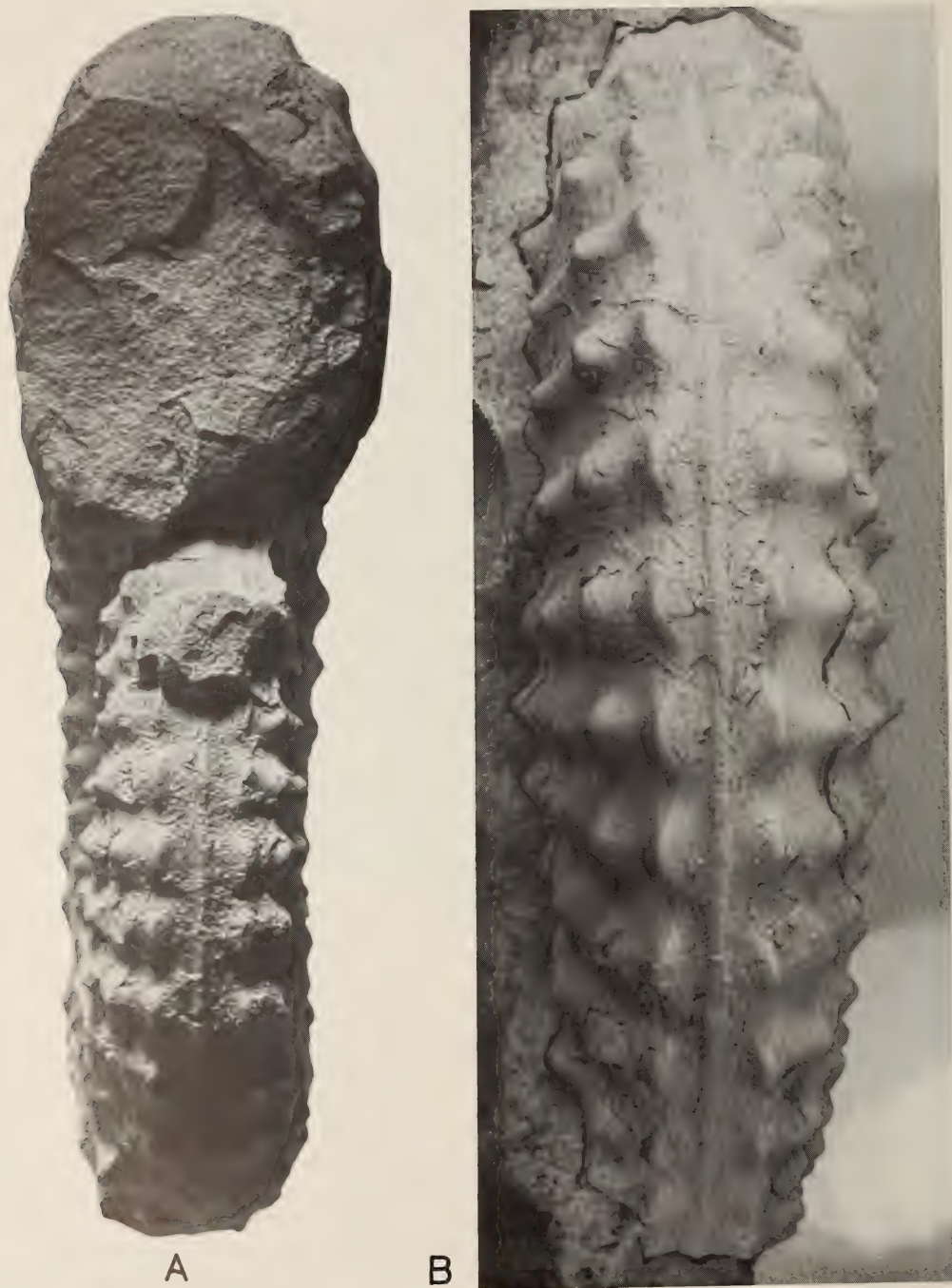


Fig. 125. *Texanites texanus* (Roemer, 1852). A. SAS-H139.  $\times 1$ . B. Unnumbered specimen in Cape Town branch of Geological Survey.



*Texanites umzambiense* sp. nov.

Figs 126–129, 152A

*Holotype*

SAM-PCP5714 (Figs 126–129), Bed C6 south of locality 1, on the southern side of the Umzamba River Estuary, Pondoland, Transkei, Umzamba Formation, Middle Santonian.

*Etymology*

Named after the Umzamba River, Pondoland, Transkei.



Fig. 126. *Texanites umzambiense* sp. nov. Holotype SAM-PCP5714.  $\times 0,59$ .

*Dimensions*

| <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|----------|------------|------------|----------------|------------|-------------|-------------|
| 221,0    | 59,0(26,7) | 66,0(29,7) | 0,89           | 99,0(44,8) | 28          | 28          |

*Description**Early whorls up to 26 mm*

The protoconch is absent, and the initial smooth stage appears to be extremely short or absent (Figs 129, 152A). Ornament consists of strong ventrolateral spines which lean against and into the umbilical wall of the succeeding whorl. On the innermost whorl preserved, these spines are impressed into the umbilical wall to such an extent that the whorl appears angular when viewed laterally. The spines arise from low, broad swellings which cover the whole flank. Spine density on the innermost two whorls is 6 and 11 per whorl respectively.

Beyond a diameter of 11 mm the whorl section becomes more angular, with a near vertical umbilical wall and weakly inflated flanks. The broad bases of the ventrolateral spines now begin forming distinct single ribs which cover the flanks of the whorls. Distinct, radially elongated umbilical tubercles start appearing at the umbilical edge. The base of each of these is elongated obliquely forward over the umbilical wall. Rib density at this stage is 21 per whorl, the interspaces being as wide as the ribs. The ventrolateral spines progressively become less prominent, and eventually appear as spirally elongated clavi in the umbilical seam.

*26 mm and beyond*

At a diameter of about 26 mm faint lateral (2) tubercles start appearing at about midflank. Simultaneously the ventrolateral clavi start migrating away from the umbilical suture to reveal the 4th row of spirally elongated tubercles. With increasing diameter the umbilical tubercles become increasingly clavate, pointing obliquely inward. The lateral tubercles eventually migrate towards the ventral third of the flanks, and the third row to the dorsal third, whilst the 4th row remains in the umbilical seam. Rib density at diameters of 62 and 135 mm is 27 and 24 per whorl respectively. On the outer phragmocone whorl complete ornament is visible (Fig. 126). The marginal (4) and external (5) tubercles are situated close together at the ventrolateral edge, and both are prominently clavate. The ventral keel is undulating, being highest in the inter-tubercular area. The preserved body chamber consists of half a whorl. There is no distinct change in ornament at the beginning of the body chamber. On the greater part of the late body chamber, ornament becomes weakened and irregular due to damage to the shell.

*Discussion*

Despite being monotypic, this species is easily distinguished from the predominantly younger species belonging to the groups of *Texanites soutoni*



Fig. 127. *Texanites umzambiense* sp. nov. Holotype SAM-PCP5714.  $\times 0,74$



and *Submortonicerias woodsi* (described below). None of these specimens has the marginal and external tubercles situated as close together as the present species, or possesses an undulating keel.

The closest ally to, and probably direct ancestor of, this species seems to be *Plesiotexanites collignoniforme* sp. nov. described above (p. 89). Both species have the marginal and external tubercles approximated, and an undulating keel. *T. umzambiense* is here separated from *P. collignoniforme* mainly because of the earlier appearance of the lateral tubercle (26 mm v.

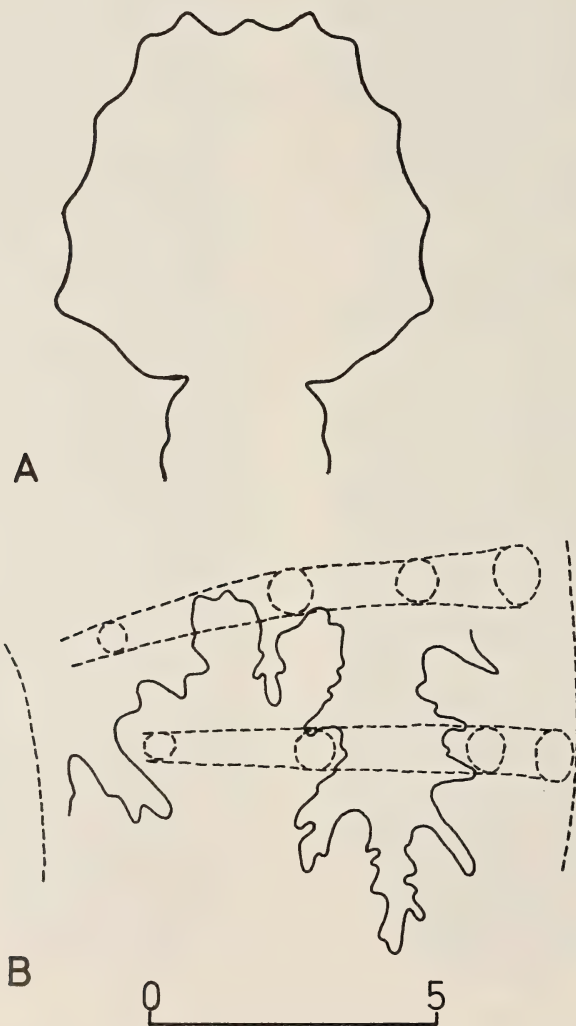


Fig. 128. *Texanites umzambiense* sp. nov. Holotype SAM-PCP5714. A.  $\times 1$ .  
B. Scale bar in millimetres.

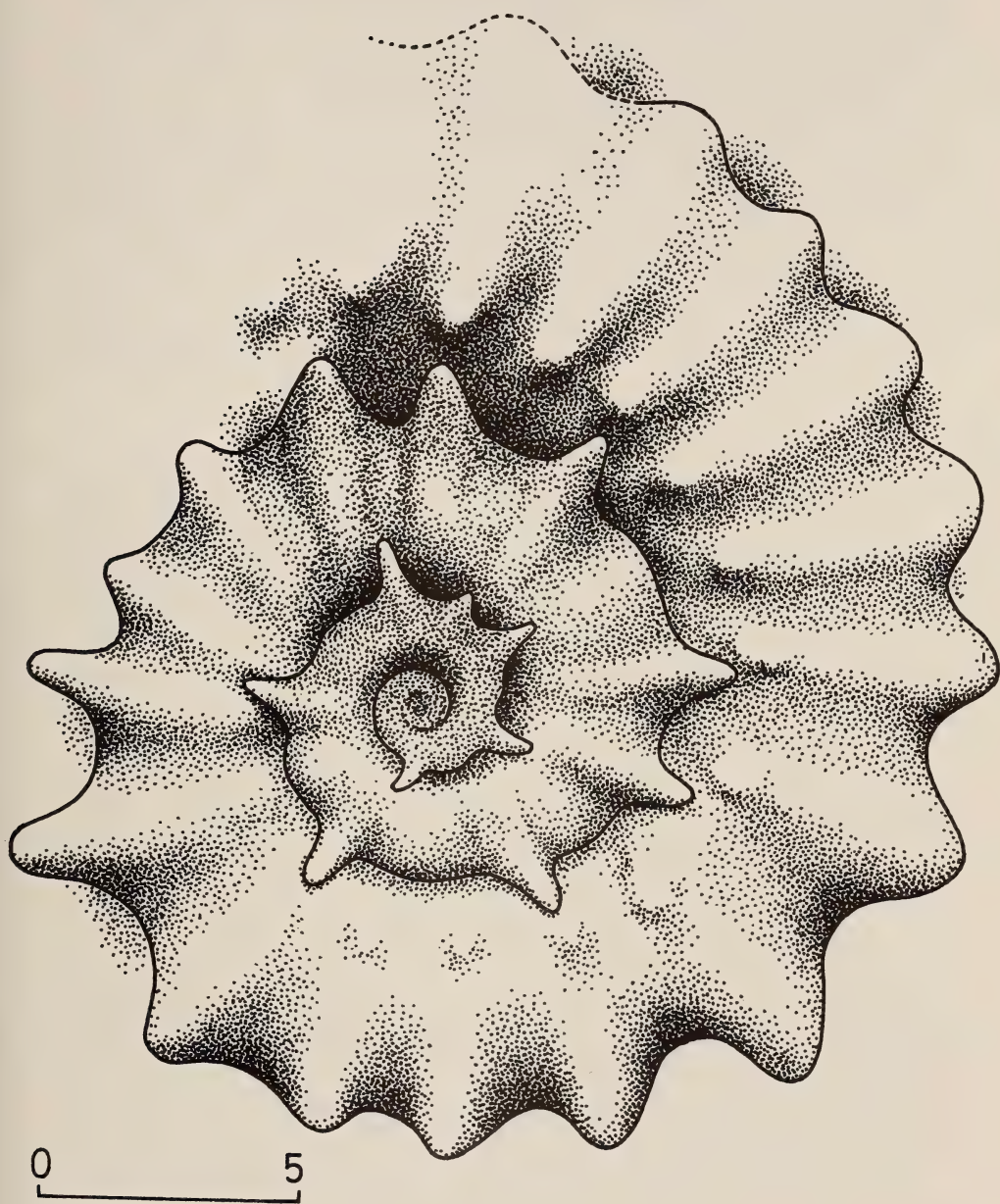


Fig. 129. *Texanites umzambiense* sp. nov. Holotype SAM-PCP5714. Drawing to illustrate early ontogeny. Scale in millimetres.

50 mm), and a more inflated whorl section on the phragmocone. Quite obviously the ontogenetic character of differentiation between *Texanites* and *Plesio-texanites* becomes evident here.

As noted above (p. 98), this could point to the beginning of the geographic separation of the Zululand and Pondoland texanite faunas.

*T. texanus hispanica*, also reported from the Umzamba Formation above (p. 162), bears superficial similarity in general form, but does not have the external and marginal tubercles as closely spaced and lacks an undulating keel.

*T. collignoni* is related in having an undulating keel, but generally has a much more compressed whorl section and different arrangement of tubercles.

*T. mikobokensis* from the Upper Santonian of Madagascar is another similarly evolute species, but has a much more compressed whorl section and different spacing of lateral ornament (see Collignon 1966a, pl. 509 (fig. 2019)).

### Occurrence

Middle Santonian of Pondoland, Transkei.

Group of *Texanites soutoni* (Baily, 1855)—*Submortonicerias woodsi* (Spath, 1921)

Texanitids of the group centred on the plexus of *T. soutoni* and *S. woodsi* form the bulk of the texanitids in the present collection, and merit special attention, not only because of numerical superiority and stratigraphic importance, but because they illustrate

- (i) what appears to be a partial geographic isolation of two contemporaneous groups within a species with some intermingling,
- (ii) a striking evolutionary sequence in both populations, spanning the period from Middle Santonian to Early Campanian, starting with a normal evolute *Texanites*, and ending with an involute *Submortonicerias*, with no clearcut break, and
- (iii) a tremendous intraspecific variation, especially as far as ornamentation and suture lines are concerned which causes one to have serious doubts about the validity of current texanitid systematics.

The texanitids occur mainly in two areas—the type section of the Umzamba Formation at the Umzamba Estuary, Transkei, locality 1 of the authors (Kennedy & Klinger 1975: 281; Klinger & Kennedy in press) and the south-eastern shores of False Bay, Zululand, at locality 105 (Kennedy & Klinger 1975: 296; herein Fig. 130) continuing the section in the cliffs at locality 74 (Kennedy & Klinger 1975: 283, fig. 8). Minor occurrences connecting the two main areas are at locality 14 (Kennedy & Klinger 1975: 283) near Umkwelane Hill, sub-surface deposits near Richards Bay at locality 6 (Kennedy & Klinger 1975: 282), and similar deposits at Durban at locality 5 (Kennedy & Klinger 1973; 1975: 282). Current evidence seems to suggest that the deposits at False Bay, Zululand, represent a deeper water facies than the shallower water transgressive facies of the Umzamba Formation.



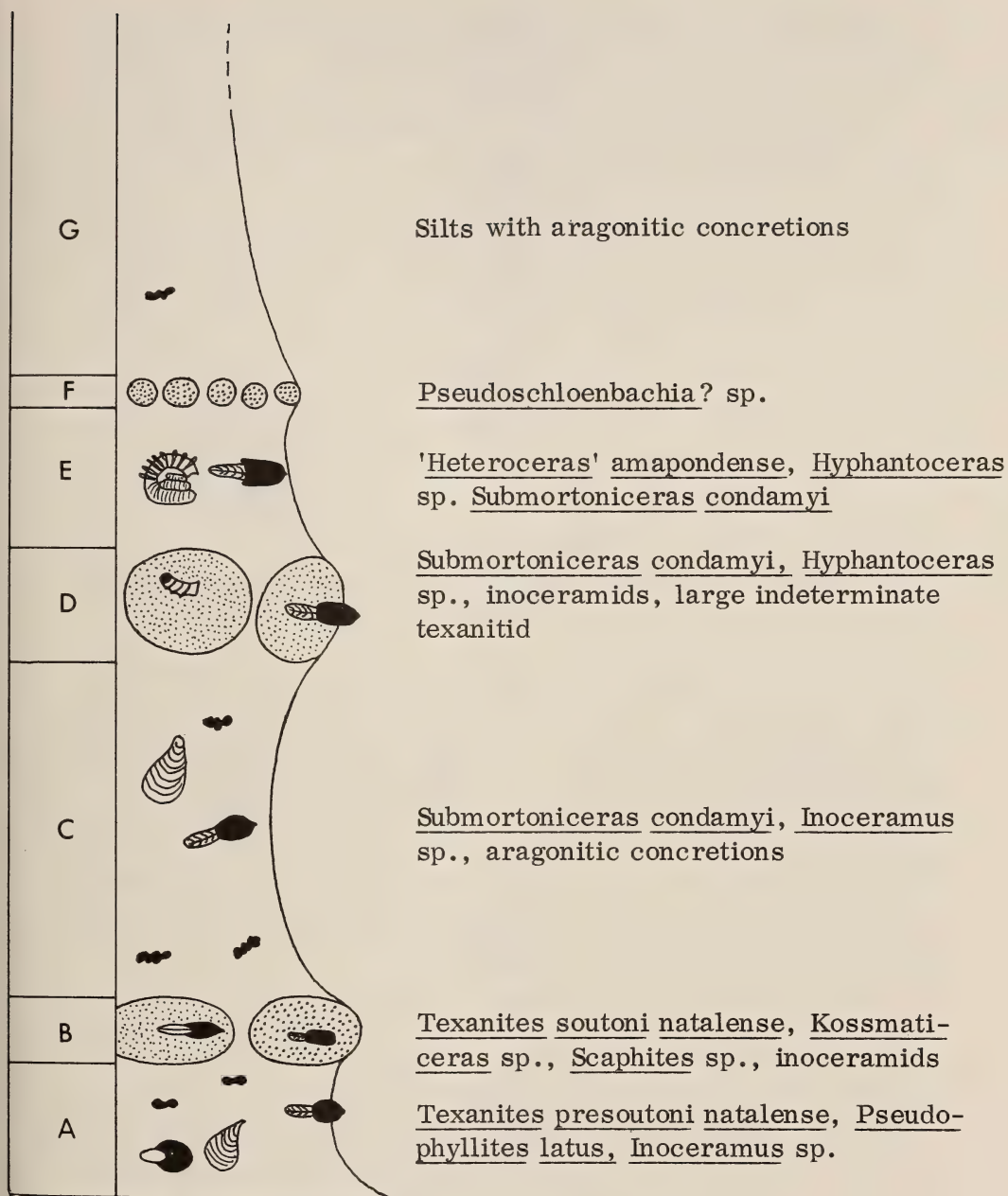


Fig. 130. Stratigraphic section at locality 105 on the south-eastern shores at False Bay.

The material is extremely variable, but data gained from detailed zonal collecting by the authors, examination of material collected zonally by Gevers, and indications of relative stratigraphic position of specimens in older collections—such as encrustation by modern epizoans indicative of a low stratigraphic position at the type section of the Umzamba Formation—permit partial interpretation of the species centred on the *T. soutoni*–*S. woodsi* plexus, both in terms of spatial and temporal variation.

At first glance, the texanitime faunas of Pondoland and False Bay appear to be completely different. This apparent 'difference' is greatly enhanced by the dissimilar lithologies and associated faunas (the latter to be discussed fully in Klinger & Kennedy in press). Specimens from False Bay generally retain calcareous white shell material in a buff-weathering sandy silt, whereas the Pondoland specimens are mainly preserved in crystalline calcite in a dark greyish-green glauconitic silt. In addition, there is a distinct difference in size between the texanitines of both areas; those from Pondoland are generally gigantic when compared with the normal-sized specimens from False Bay.

Detailed stratigraphic collecting shows that there is a distinct trend in both faunas towards acquisition of submortoniceratine shell-form (Figs. 131–132). True texanitids with umbilical diameters of the order of *c.* 45 per cent occur near the bases of both sections, and through gradually decreasing umbilical width and whorl breadth, give way to true submortoniceratids towards the higher levels in the sections.

Apart from differences in size, real differences are to be found in the mode of acquisition of *Submortoniceratas* ornament, and in the relative width of the lobes of the suture lines. In Pondoland, the submortoniceratine characters are developed in the 'traditional' way, i.e. through gradual weakening of ornament from the inside outwards. At False Bay, however, a great proportion of specimens has inner whorls with ornament weaker than that of the outer whorls and retains tuberculation on part of the body chamber. It may thus be said that submortoniceratine characteristics are acquired caenogenetically in Pondoland, but proterogenetically at False Bay. As far as suture line is concerned, the False Bay specimens generally have much wider and shallower lobes exposed on the flanks than their Pondoland counterparts.

Detailed examination of the associated fauna, however, has shown that the stratigraphic interval exposed at the type section of the Umzamba Formation up to Bed A7–8 (Klinger & Kennedy in press) corresponds approximately to that exposed at locality 105 and the higher parts of the section at locality 74 (Kennedy & Klinger 1975: 293, fig. 8). Furthermore, typical, though sometimes dwarfed or smaller, Pondoland faunas occur in the Richards Bay and Umkwelane Hill areas, and even at False Bay, while typical False Bay faunas occur at Umkwelane Hill, indicating an area of intermingling between apparently isolated faunas.

The authors are now able to correlate the texanitime faunas of Pondoland and Zululand, and it is now possible to produce a series of specimens of more or less equal involution and age, ranging from completely smooth to coarsely

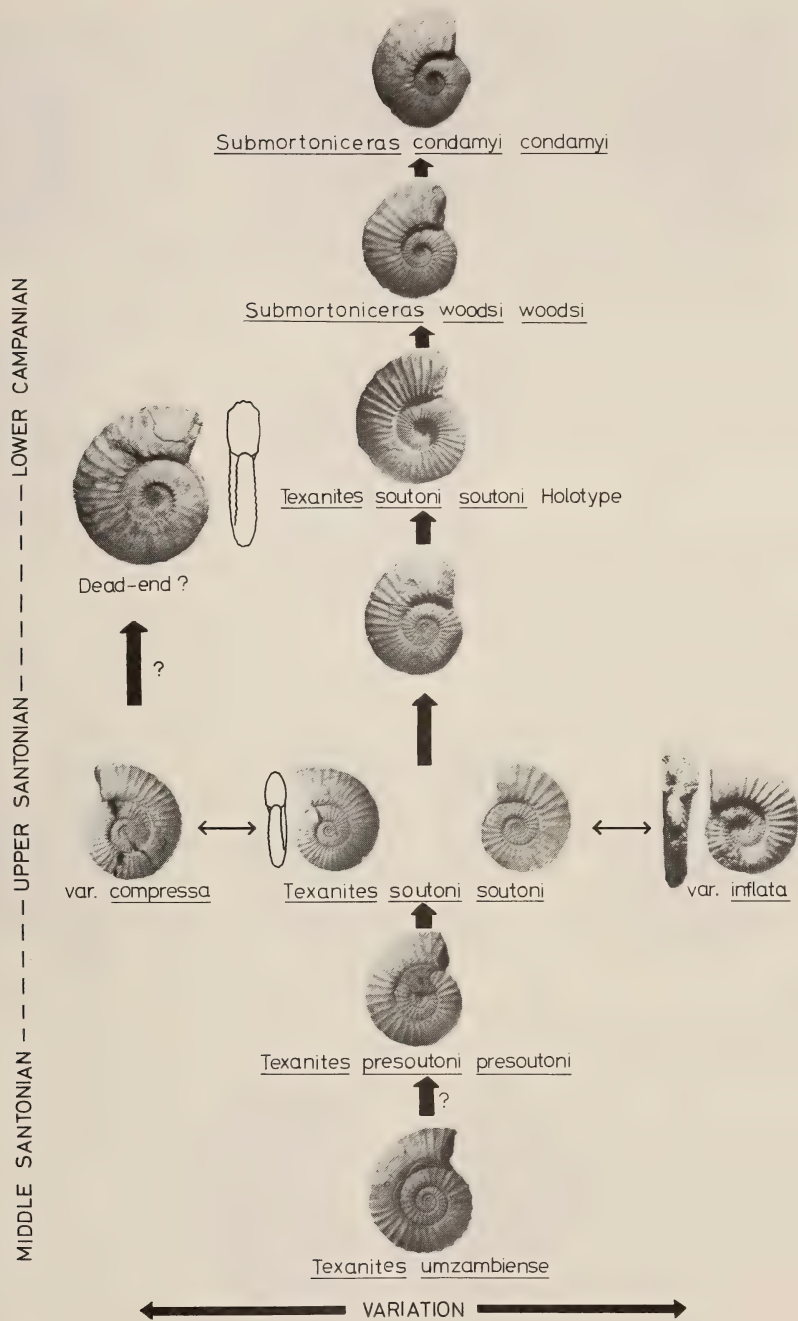


Fig. 131. Diagrammatic illustration showing suggested lines of evolution and intraspecific variation in species of the *Texanites soutoni*-*Submortonicerases woodsi* plexus at the type section of the Umzamba Formation.



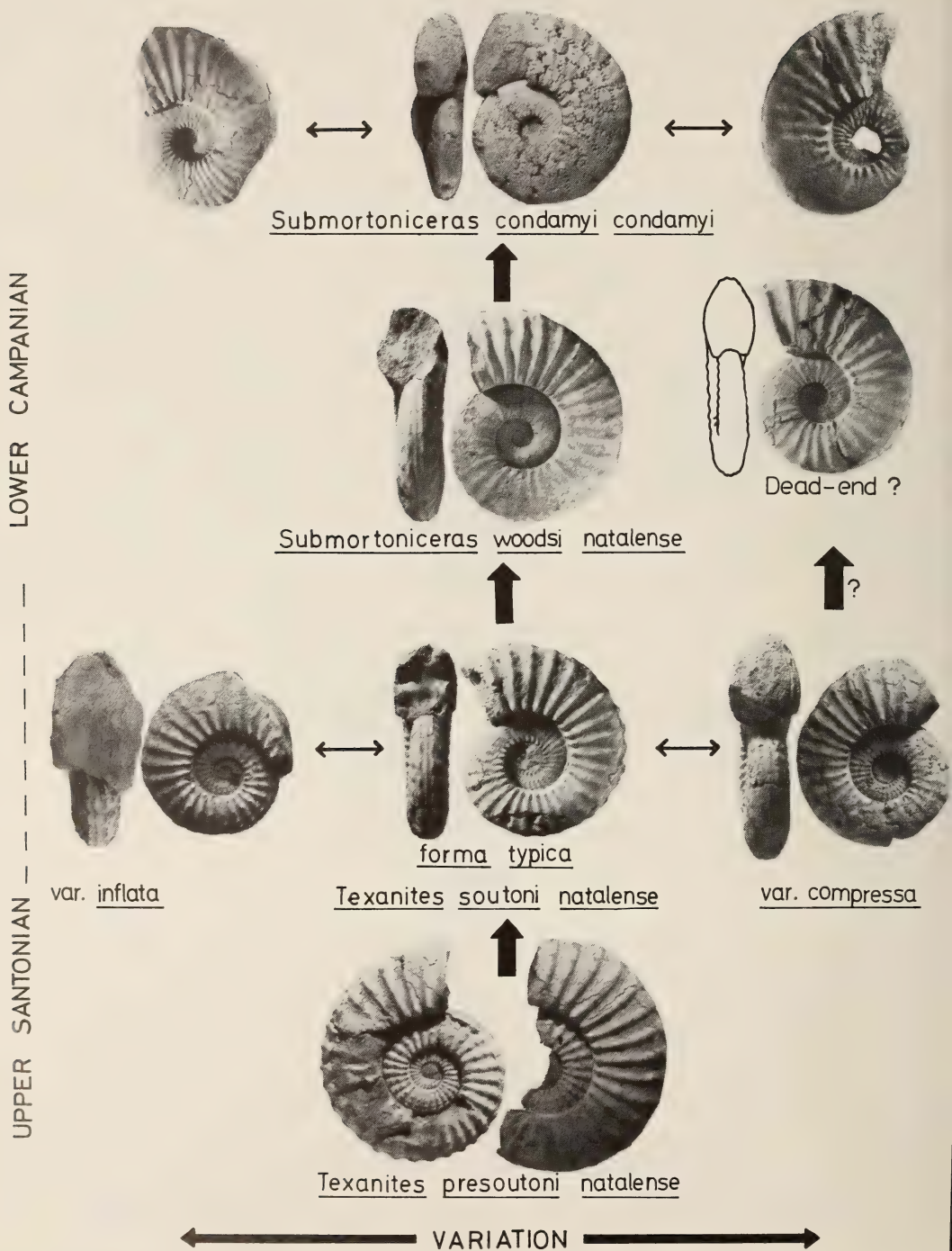


Fig. 132. Diagrammatic illustration showing suggested lines of evolution and intraspecific variation in species of the *Texanites soutoni*-*Submortonicerases woodsii* plexus in the False Bay region of Zululand.

ornamented on the inner whorls, all occurring at the same stratigraphic level.

The extreme variation at the same stratigraphic level, combined with the lack of abrupt vertical changes in the population, makes it difficult to differentiate satisfactorily between the various groups. As there are no visible abrupt changes in the population, differentiation will have to be arbitrary, and here umbilical width seems to be the most feasible choice. The Pondoland and Zululand faunas, where sufficiently different, are separated at subspecific level. On the latter basis, the following morphological taxa may be recognized:

U = c. 45% with external and marginal tubercles separated and ribbing predominantly single, especially on the body chamber = *T. presoutoni* sp. nov.

*T. presoutoni presoutoni* ssp. nov. Holotype is SAM-PCP5712 from the Umzamba Formation, Umzamba Cliff at locality 1, presumably Bed A1.

*T. presoutoni natalense* ssp. nov. Holotype is SAS-H126A/12 from the St Lucia Formation, locality 105, Bed A.

U = c. 40% = *T. soutoni* s.l.

*T. soutoni soutoni* (Baily, 1855). Holotype is the specimen figured by Baily (1855, pl. 11, fig. 1a-c), here refigured as Figure 143.

*T. soutoni natalense* ssp. nov. Holotype is SAS-H126B/3 from the St Lucia Formation, locality 105, Bed B.

In both the above subspecies an inflated and compressed variety may be recognized, both apparently with a tendency towards acquisition of submortoniceratine characters, but it appears the compressed variety is a dead-end. (See Figs 131-132.)

U = c. 35% = *Submortonicerat* *woodsii* s.l.

*S. woodsii woodsii* (Spath, 1921). Holotype is SAM-5451 from Umkwelane Hill, Zululand, the specimen figured by Spath (1921, pl. 21 (fig. 1a-d)), here refigured as Figure 186.

*S. woodsii natalense* ssp. nov. Holotype is SAS-Z1875 from the St Lucia Formation, locality 105.

U = c. 30% = *S. condamyi*.

*S. condamyi condamyi* Collignon. Lectotype herein designated is the specimen figured by Collignon (1948, pl. 18(12) (fig. 2-2b)) from the Lower Campanian of Berere, Madagascar.

*S. condamyi umzambiense* ssp. nov. Holotype is SAM-PCP5717 from the Umzamba Formation, Umzamba Cliff, locality 1, Bed A7.

This framework (see also Figs 131-132) should be seen as a *working basis* towards classifying the species centred on *T. soutoni*-*S. woodsii*, and not as a rigid, compartmentalized framework. Many of the specimens discussed below could be referred to more than one species or subspecies. This is in part due to the extreme horizontal variation and also the continuous vertical transition from one species to another. In addition, this classification is hampered by the fact that it has to accommodate the holotypes of established species which in

themselves are already transitional between species (or even genera), e.g. *T. soutoni* or incomplete, e.g. *S. woodsi*. Material described by Young (1963) from the Gulf Coast of America also falls within the range of variation of this species group, and has to be accommodated.

*Texanites presoutoni presoutoni* ssp. nov.

Figs 133–137, 152C

*Mortoniceras soutoni* (Bailey): Woods, 1906: 337, pl. 43 (fig. 1). ?Van Hoepen 1921: 38 *pars*, pl. 11 only.

*Holotype*

SAM-PCP5712 (Figs 133–135), locality 1, basal beds at Umzamba Cliff, Pondoland, Transkei, Umzamba Formation, Upper Santonian.

*Material*

SAM-4828, locality 1, basal beds at Umzamba Cliff, Pondoland, Transkei; and BMNH-C19447 from an unknown horizon at the same locality, Umzamba Formation, Upper Santonian.

*Dimensions*

|         | <i>D</i> | <i>Wh</i> | <i>Wb</i>   | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|---------|----------|-----------|-------------|----------------|-------------|-------------|-------------|
| PCP5712 | 387,0    | —         | 122,0(31,5) | —              | 181,0(46,8) | 30          | 30          |
| SAM4828 | 230,0    | —         | 81,0(35,2)  | —              | 97,0(42,0)  | 27          | 27          |

*Description*

The material, though limited in numbers, is very varied. Coiling is loose, with an umbilical diameter of 42 to 47 per cent. The whorl section may be quadrate in the very early stages, but later becomes compressed, higher than wide throughout.

SAM-PCP5712 (Figs 133–135, 152C) has the innermost whorls preserved, illustrating the ontogenetic development. After the initial smooth stage, long spinose ventrolateral tubercles appear, leaning against the umbilical wall. Smaller umbilical (1) tubercles appear next, followed by lateral (2) tubercles at a diameter of *c.* 20 mm.

Ornament remains basically the same throughout the rest of the phragmocone, though differing considerably in terms of strength and spacing. SAM-PCP5712 (Fig. 133) thus has much coarser ornament on the phragmocone than SAM-4828 (Fig. 136). BMNH-C19447 (Fig. 137) has as sparse costation as SAM-PCP5712 (Fig. 133), but by no means as strongly developed tuberculation.

All the specimens have single ribbing throughout—a feature here considered as being ‘primitive’.

Towards the body chamber the lateral (2) and submarginal (3) tubercles become effaced, and on the later part all ornament weakens.

The suture varies, but has stout saddles *E/L* and *L/U*<sub>2</sub> and long, thin lobes *L* and *U*<sub>2</sub>.





Fig. 133. *Texanites presoutoni presoutoni* sp. nov. Holotype SAM-PCP5712.  $\times 0,35$ .



Fig. 134. *Texanites presoutoni presoutoni* sp. nov. Holotype SAM-PCP5712. Close-up of inner whorls to illustrate ontogeny.

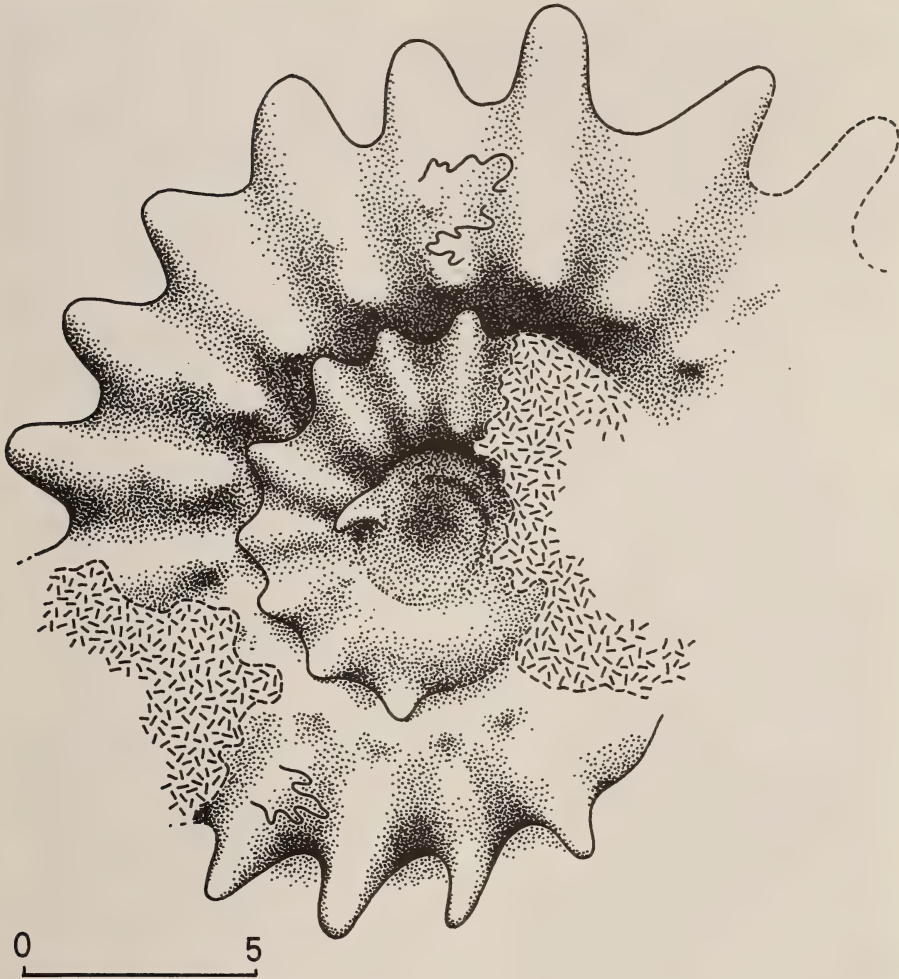


Fig. 135. *Texanites presoutoni presoutoni* sp. nov. Drawing of inner whorls based on holotype.

#### Discussion

The status of this species is admittedly somewhat artificial, but forms a convenient starting point for describing the species of the *T. soutoni*-*S. woodsi* plexus.

The specimen figured by Van Hoepen as *Mortoniceras soutoni* (1921, pl. 11) has ornament on the inner whorls closely resembling that of the holotype of the species, but denser, flexuous ribbing on the body chamber and an umbilical width of *c.* 43 per cent. It should probably also be referred to the present species, but the authors have not been able to trace it in the Transvaal Museum for





Fig. 136. *Texanites presoutoni presoutoni* sp. nov. Paratype SAM-4828.  $\times 0,6$  The specimen figured by Woods (1906, pl. 43 (fig. 1)).

definite identification. Haas (1942: 17) had already suggested that Van Hoepen's figured specimen be separated from *T. soutoni* as variety *densicosta*. Apart from the fact that this cannot be accepted as a valid designation, the term *densicosta*, should it be accepted in formal nomenclature, is extremely misleading, as in this case it applies only to the body chamber ornament. The authors' comments on this specimen (Klinger & Kennedy 1977: 97) are still partially valid, but in suspecting different ontogenetic development the authors



Fig. 137. *Texanites presoutoni presoutoni* sp. nov. Paratype BMNH-C19447.  $\times 1$ .

were misled by differences in preservation and the extreme intraspecific variation in *T. soutoni*.

Both Haas (1942: 12) and Young (1963: 85) regarded Woods's figured specimen (SAM-4828) of *Mortoniceras soutoni* as not being conspecific with the holotype, but gave no reasons for this. The wide umbilicus, single ribbing throughout and long, narrow lobes in the suture of this specimen are all characteristic of the present subspecies.

*T. presoutoni presoutoni* is closely connected to *T. soutoni soutoni* by specimens such as SAM-PCP5713 and SAM-PCP5718 (Figs 144-145) with only a few bifurcations and a slightly narrower umbilicus.

*T. presoutoni* s.s. differs from its subspecies in the False Bay region of Zululand, *T. presoutoni natalense*, mainly in losing tuberculation on the body chamber, whereas the latter remains tuberculate. The Pondoland subspecies attains larger dimensions. \*

#### Occurrence

Lower part of Upper Santonian of Pondoland, Transkei.

#### *Texanites presoutoni natalense* ssp. nov.

Figs 138, 139B, 140-142

#### Holotype

SAS-H126A/12 (Figs 138, 139B), Bed A locality 105, south-eastern shores of False Bay, Zululand, St Lucia Formation, Upper Santonian.

#### Material

Paratypes are SAS-Z1140 and SAM-PCZ5885, both from the same locality as the holotype.

#### Dimensions

|          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>   | <i>Wb: Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|------------|-------------|---------------|-------------|-------------|-------------|
| H126A/12 | 301,0    | —          | 106,0(35,2) | —             | 130,0(43,2) |             | 17 × 2      |
| Z1140    | 226,0    | 62,0(27,4) | 76,0(33,6)  | 0,81          | 101,0(44,7) | 31          | 31          |
| PCZ5885  | 177,0    | 51,0(28,8) | 62,0(35,1)  | 0,82          | 75,0(42,4)  | 28          | 27          |

#### Description

Coiling is evolute, with an umbilical width of 42 to 44 per cent of the total diameter. The whorl section is massive, higher than wide throughout with a near vertical umbilical wall, and, in intercostal section, little-inflated flanks converging to a broadly rounded venter. Maximum whorl breadth is near the dorsal third of the flanks in intercostal section, and in costal section at the site of the lateral tubercle, which is very prominent.

Ornament on the phragmocone consists of radially elongated umbilical tubercles (1), arising at the umbilical edge, and progressively clavate lateral, submarginal, marginal and external (2-5) tubercles. At larger diameters on the





Fig. 138. *Texanites presoutoni natalense* ssp. nov. Holotype SAS-H126A/12.  $\times 0,53$ .



Fig. 139. A. *Submortonicer as woodsi* (Spath, 1921). SAS-Z1138.  $\times 0,57$ . B. *Texanites presoutoni natalense* ssp. nov. Holotype SAS-H126A/12.  $\times 0,58$ .



Fig. 140. *Texanites presoutoni natalense* ssp. nov. Paratype SAS-Z1140.  $\times 0,6$ .

phragmocone the lateral (2) tubercles may become conical to radially elongated, as the umbilical ones. Bifurcations are not very common on the late part of the phragmocone. On the body chamber ribbing becomes narrower, but lateral and submarginal (2 and 3) tuberculation does not become effaced.

The suture consists of blocky saddles and narrow lobes, but proportions vary considerably in three available specimens. The lateral lobe (L) is long, narrow and trifid, with a bifid median prong in the holotype (Fig. 142), but wider and shorter in paratype SAM-PCZ 5885 (Fig. 141).





Fig. 141. *Texanites presoutoni natalense* ssp. nov. Paratype SAM-PCZ5885.  $\times 0,6$ .

### Discussion

Of the three available specimens, only the holotype has the body chamber preserved, which shows the presence of the full complement of ornament thus distinguishing it from its Pondoland counterpart, *T. presoutoni presoutoni*. Apart from this, the general mode of ornament on the phragmocone, shell shape and suture line are compatible. The two paratypes, with occasional bifurcations, are already transitional to *T. soutoni natalense* ssp. nov. (described below), and may be compared with Pondoland specimens such as SAM-PCP5718 (Fig. 144) which are transitional between *T. presoutoni* s.s. and *T. soutoni* ss.

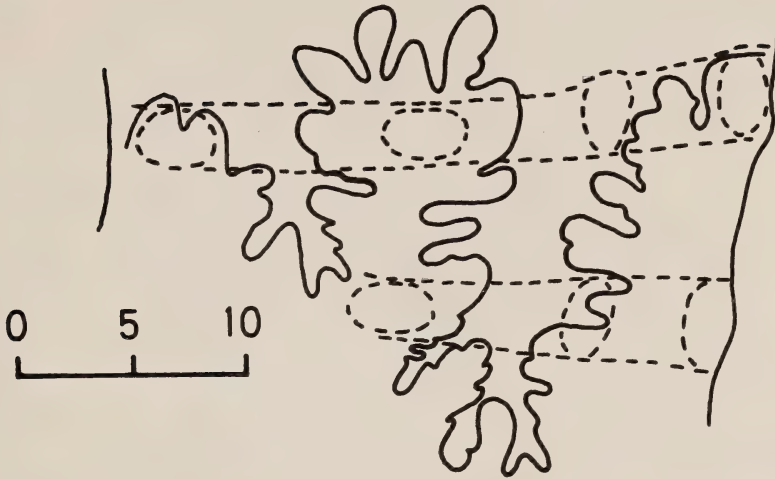


Fig. 142. *Texanites presoutoni natalense* ssp. nov. Holotype SAS-H126A/12. Suture line. Scale bar in millimetres.

#### Occurrence

Upper Santonian of Zululand.

#### *Texanites soutoni soutoni* (Baily, 1855)

Figs 143–151, 152B, 153–163

*Ammonites soutoni* Baily, 1855: 455, pl. 11 (fig. 1a–c).

*Mortoniceras soutoni* (Baily): Spath, 1921: 234, pl. 20 (fig. 4); 1922: 136, pl. 7 (fig. 4). Van Hoepen, 1921: 38, pl. 10 (*non* pl. 11 = *T. presoutoni* s.s. sp. nov.).

*Non Mortoniceras soutoni* (Baily): Woods, 1906, 337, pl. 43 (fig. 1a–b) (= *T. presoutoni* s.s. sp. nov.).

*Texanites soutoni* (Baily): Matsumoto, 1955: 42, text-fig. 3. Collignon, 1966: 70, pl. 483 (fig. 1956). Klinger & Kennedy, 1977: 89, fig. 9.

*Non Mortoniceras* sp. aff. *soutoni* Spath, 1922: 235 (= *T. soutoni natalense* ssp. nov.).

? *Mortoniceras* aff. *soutoni* Spath, 1925: 199.

? *Texanites* cf. *soutoni* Collignon, 1948: 78, pl. 9(3) (fig. 1a–b).

*Non Texanites soutoni* (Baily): Kennedy & Klinger, 1972: pls 72–73 (with *Spinaptychus*) (= *T. soutoni natalense* ssp. nov.).

#### Type

Holotype is BMNH-C47261, the specimen figured by Baily (1855, pl. 11 (fig. 1)), here refigured as Figure 143, locality 1, Umzamba Cliff, Pondoland, Transkei, Umzamba Formation, Upper Santonian.

#### Material

SAM-PCP5713–5715, PCP5718, SAM-13090, SAM-7076–7077, SAS-P747, P1334, P1398, NMB-D1605a–b, BMNH-C19442, C19454, C19461, C47261, all from locality 1, Umzamba Cliff, Pondoland, Transkei, Umzamba Formation, Middle to Upper Santonian; SAS-Z306 and SAM-PCZ5885,



Fig. 143. *Texanites soutoni soutoni* (Baily, 1855). Photograph of cast of holotype, BMNH-C47261.  $\times 0,34$ . Note that Baily's figure is a mirror image.



locality 14, near Mfolozi, St Lucia Formation, Santonian II–III to Campanian I; SAM-PCZ5884, locality 6, excavations near Richards Bay, St Lucia Formation, Santonian II–III to Campanian I; SAM-PCZ 5903, locality 74, Die Rooiwalle, Zululand, St Lucia Formation, Santonian to Campanian; and possibly SAM-FB from an unknown locality in False Bay, probably also locality 74.

### Dimensions

|          | <i>D</i> | <i>Wb</i>   | <i>Wh</i>   | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|-------------|-------------|----------------|-------------|-------------|-------------|
| PCP5714  | 231,0    | 66,0(28,6)  | 74,0(32,0)  | 0,89           | 107,0(46,3) | 30          | 30          |
| PCP5713  | 200,0    | 56,0(28,0)  | 70,0(35,0)  | 0,80           | 82,0(41,0)  | 28          | 28          |
| SAM-7077 | 337,0    | —           | 106,0(31,5) | —              | 149,0(44,2) | 38          | 38          |
| P747     | 357,0    | 78,0(21,8)  | 131,0(36,7) | 0,59           | 145,0(40,6) | 36          | 36          |
| P1334    | 329,0    | 89,0(27,1)  | 110,0(33,4) | 0,81           | 140,0(42,6) |             | 22 × 2      |
| D1605b   | 259,0    | —           | 93,0(35,9)  | —              | 105,0(40,5) | 30          | 30          |
| PCP5718  | 356,0    | —           | 127,0(35,7) | —              | 151,0(42,4) | 30          | 32          |
| Z306     | 237,0    | 66,0(27,8)  | 93,0(39,2)  | 0,71           | 91,0(38,4)  | 26          | 30          |
| C47261   | 444,5    | 114,3(25,7) | 152,4(34,3) | 0,75           | 177,8(40,0) | 35          | 37          |

### Diagnosis

Texanitid with umbilical width of approximately 40 per cent of total diameter, whorl section higher than wide throughout; with venter narrower than dorsum. Ornament on innermost whorls variable, ranging from virtually smooth to strong, with variable number of bifurcations. Towards the body chamber lateral ornament becomes attenuated. Generally one or two bifurcations on outer body chamber whorl. Suture variable.

### Description

As here interpreted, the species is very variable, consequently ample illustrations are provided in lieu of lengthy descriptions.

Two varieties within the species may be recognized, both occurring together near the base of the section exposed at Umzamba Cliff: an inflated broad-whorled variety, e.g. SAM-PCP5718 (Figs 144–145), and a more evolute, slender-whorled and compressed variety, e.g. SAM-7077 (Fig. 146), which may here be labelled var. *inflata* and var. *compressa* for descriptive purposes. Both extremes, however, are connected by specimens such as SAS-P747 (Figs 147–148) and SAS-P1334 (Fig. 149). Specimens SAM-7077 (Fig. 146), SAS-P747 (Fig. 147) and SAS-P1334 (Fig. 149) illustrate the variation in strength of ornament in the species. Details of these differences in the ontogeny are discussed below. Stratigraphic data seem to suggest that the holotype of *T. soutoni* s.s. may be derived from variety *inflata* through reduction of the umbilical diameter, probably via specimens such as SAM-PCP5715 (Fig. 150). Variety *compressa* possibly also evolved in the direction of *Submortonicerias* via a specimen such as SAM-7076 (Fig. 151) with attenuated ornament on the outer whorls but a relatively wide umbilicus. This latter trend appears to have been a dead-end (Fig. 131), whereas forms such as the holotype of *T. soutoni* s.s. gradually evolved into *Submortonicerias woodsi*.



Fig. 144. *Texanites soutoni soutoni* (Baily, 1855). SAM-PCP5718. Variety here referred to informally as var. *inflata*.  $\times 0,41$ .

Preservation of material at the Umzamba Estuary is generally much better than that of temporally equivalent strata in Zululand, and a number of specimens have the inner whorls preserved, permitting a full description of the ontogeny of the species. None of the specimens, however, has the protoconch preserved.

Details of the ontogeny are illustrated in Figures 152–153. Even on the



Fig. 145. *Texanites soutoni soutoni* (Baily, 1855). SAM-PCP5718. Variety here referred to informally as var. *inflata*.  
× 0,48.





Fig. 146. *Texanites soutoni soutoni* (Baily, 1855). SAM-7077. Variety here referred to informally as var. *compressa*.  $\times 0,41$ .

innermost whorls differences in strength of ornament are obvious when comparing SAM-PCP5713 (Fig. 152B) with SAS-P747 (Fig. 153C). The initial smooth stage is short, except in SAS-P747, where it persists to a diameter of about 10 mm. The ventrolateral tubercles develop first, and in most cases occur as long, curved spines with broad bases leaning against the umbilical wall. In this respect SAS-P747 (Fig. 153C) seems to differ from the rest of the specimens in appearing to lack the strong development of ventrolateral spines. Close investigation of the inner whorls of SAS-P747 (Fig. 153C), however,



Fig. 147. *Texanites soutoni soutoni* (Baily, 1855). SAS-P747. Specimen connecting between varieties *compressa* and *inflata* in having a very compressed whorl section, but not as evolute coiling.  $\times 0,42$ .



Fig. 148. *Texanites soutoni soutoni* (Baily, 1855). SAS-P747. Specimen connecting between varieties *inflata* and *compressa* in having extremely compressed whorls, but relatively narrow umbilicus.  $\times 0,5$ .





Fig. 149. *Texanites soutoni soutoni* (Baily, 1855). SAS-P1334. Specimen connecting between varieties *inflata* and *compressa*, and with very weak lateral ornament.  $\times 0,55$ .



Fig. 150. *Texanites soutoni soutoni* (Baily, 1855). SAM-PCP5715.  $\times 0,41$ .

reveals the vestiges of two tubercles and corresponding indentations on the umbilical wall of the succeeding whorl, indicating that spines could have been present and that their absence could be partially due to the state of preservation. Small, rounded umbilical tubercles occur next, followed by a row of lateral tubercles. With increasing diameter the ventrolateral spines in the umbilical suture become smaller and more clavate, and migrate away from the umbilical wall to expose a fourth row of tubercles on the flanks. Thereafter ornament remains basically the same, although details differ, as shown in the Figures.



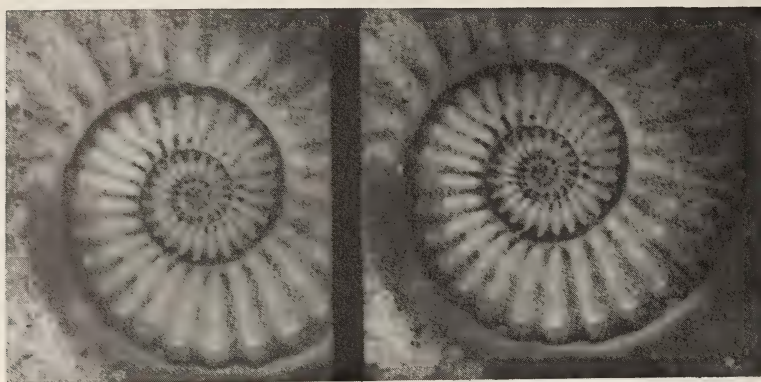
Fig. 151. *Texanites soutoni soutoni* (Baily, 1855). SAM-7076. Specimen with attenuated ornament, trending towards *Submortonicer*, but apparently a dead-end lineage.  $\times 0,42$ . (See also Fig. 131.)

The suture is very variable as Van Hoepen (1921) had already noted. Apart from differences in the length and width of the second lateral saddle ( $L/U_2$ ) already discussed and figured by Van Hoepen (1921), the most obvious and easiest recognizable differences are to be found in the length and incision of the saddles and lobes exposed on the flanks. Data here are scant, but it appears as if there is a tendency towards greater complexity of the suture line higher up in the stratigraphic sequence (Fig. 161) leading towards the formation of the





A



B



C

Fig. 152. Stereopair photographs of inner whorls of specimens to illustrate ontogenetic development. A. *Texanites umzambiense* sp. nov. Holotype SAM-PCP5714. B. *Texanites soutoni soutoni* SAM-PCP5713. C. *Texanites presoutoni presoutoni*. Holotype SAM-PCP5712.



A



B



C

Fig. 153. Stereopair photographs of inner whorls of specimens of *Texanites soutoni soutoni* to illustrate the ontogenetic variation. A. SAM-7077. B. SAS-P1398. C. SAS-P747.



Fig. 154. *Texanites soutoni soutoni* (Baily, 1855). SAS-Z306. A dwarfed specimen from the environs of Umkwelane Hill.  $\times 0,56$ .

narrow-stemmed, deeply incised saddles and lobes of *Submortonicer* *woods* and *S. condami*. The lateral lobe (L) appears to become shorter and wider with splayed ends, and to change from subtrifid to more symmetrically bifid. Comparison of the sutures of *T. presoutoni* s.s. (specimens SAM-PCP5712 and SAM-4828, both from the lower parts of the sequence at Umzamba), through normal representatives of *T. soutoni* s.s. (SAS-PCP5718, SAS-P747 and NMB-D1605B) and the holotype of *T. soutoni* s.s. (C47261 and a related form, SAM-PCP5715) through to *Submortonicer* *woods* *woods* and *S. condami*





Fig. 155. *Texanites soutoni soutoni* (Baily, 1855). SAS-Z306. A dwarfed specimen from the environs of Umkwelane Hill.  $\times 0,66$ .

*umzambiense* seems to illustrate the point (Fig. 161).

As far as can be ascertained, there seems to be no direct relationship between complexity of suture line and ornament.

#### *Discussion*

Despite being one of the first ammonites to be described from the Cretaceous deposits at the Umzamba Estuary, this species has been consistently misinterpreted. Both Spath (1922: 136) and Van Hoepen (1921: 38–45) commented on the extreme variation of *T. soutoni* in their collections. Whereas



Fig. 156. ? *Texanites soutoni soutoni* (Baily, 1855). SAM-PCZ5903, from Die Rooiwalle, Zululand.  $\times 0,68$ .

Spath concentrated mainly on density and character of ribbing (presence or absence of bifurcations) and to a lesser extent on the tightness of coiling, Van Hoepen paid close attention to the configuration of the suture lines and came to the conclusion that, in some cases at least, the comparative significance of the suture line at more or less the same age is fiction. Apart from these two authors, little substantial research has been done on this species.

The largest known collections of *T. soutoni* are housed in the collections of the British Museum (Natural History), the South African Museum, Geological Survey of South Africa (Pretoria), and the Transvaal Museum. Examination of these collections, virtually all from the Umzamba Estuary, shows that hardly two specimens are alike. The sediments at Umzamba represent a condensed sequence (Klinger & Kennedy 1977: 105, and in press). Stratigraphic data are thus essential for meaningful systematics. Unfortunately very little stratigraphic data are available in the literature. Baily (1855: 455) stated of the holotype that Thomas Souton had 'extracted it . . . from a very hard stratum high up the cliff'. Griesbach (1871: 62 (table)) lists *Ammonites soutoni* as occurring in his Bed d. Plows (1921: 63) recorded a specimen of *Mortoniceras soutoni* in his Bed 14. Rogers & Schwarz (1902: 41) and Gevers (in Rennie 1930: 253) record *Mortoniceras soutoni* from the basement beds at Umzamba.

Detailed collecting by the authors at the type section of the Umzamba Formation, examination of the material collected zonally by Gevers, and indications of relative stratigraphic position of specimens in older collections, such as encrustation by modern epizoans, indicative of a low horizon at the type section which is inundated by the present sea during high tide, permitted partial explanation of the species plexus centred on *T. soutoni* as outlined above (Fig. 131). The 'high horizon' ascribed to the holotype of *T. soutoni* by Baily tallies well with the present interpretation that submortoniceratine characteristics are acquired *gradually* through decreasing umbilical width and progressive loss of ornament in earlier stages when passing higher up through the sequence exposed at the Umzamba Estuary.

The question of whether Baily's *Ammonites soutoni* should be referred to *Submortoniceras*, as advocated by Spath (1953: 52) and Young (1963: 91), or *Texanites*, following Matsumoto (1955: 42, 1970: 279) or Collignon (1948: 42, 1966a: 70), thus becomes academic, depending on where the boundary between *Texanites* and *Submortoniceras* is drawn. According to the present classification, the holotype of *Ammonites soutoni* is referred to the genus *Texanites*.

A complete, though dwarfed, specimen SAS-Z306 (Figs 154-155) from locality 14 at Umkwelane Hill represents the first recording of this species from Zululand.

SAM-PCZ5903 (Fig. 156) and SAM-FB (Fig. 157) are the only two possible representatives of the nominate subspecies from the northern part of Zululand at Die Rooiwal, locality 74.

Specimen SAM-5491 (Fig. 81) described by Spath (1921: 234) as *Mortoniceras* aff. *umkwelanense* and considered related to *T. soutoni*, certainly does not



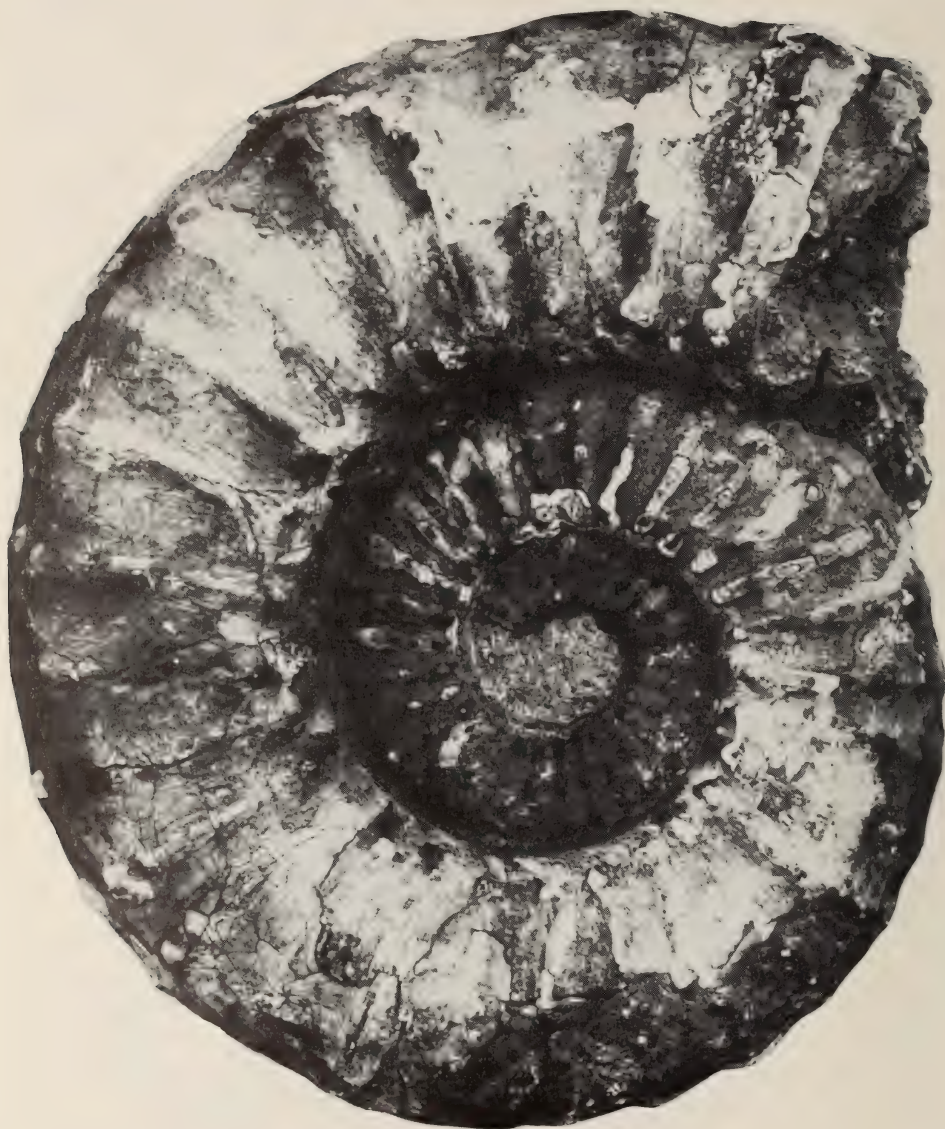


Fig. 157. ? *Texanites soutoni soutoni* (Baily, 1855). SAM-FB, a very large specimen, possibly referable to the nominate subspecies from an unknown locality at False Bay, Zululand.  
× 0,48.



Fig. 158. *Texanites* sp. aff. *soutoni* (Baily, 1855). TM1491, from an unknown locality in Mozambique.  $\times 1$ .



belong to this species, but is an example of *Plesiotexanites matsumotoi* sp. nov. described above.

The specimen described by Spath (1921: 235) as *Mortonicer* aff. *soutoni* from Umkwelane Hill, Zululand, belongs to the group of *T. soutoni* s.l. but is better referred to *T. soutoni natalense* ssp. nov. on account of the smooth inner whorls.

Two very corroded specimens, TM1491 (Fig. 158) and TM1493 (Fig. 159), described by Spath (1925: 199–200) as *Mortonicer* aff. *soutoni*, are very doubtful contenders. Apart from the fact that they were found in 'Maputoland' (Mozambique) and presented to the Transvaal Museum by a 'Señor Morreira', no other locality data are available. In view of their poor state of preservation a definite identification is not possible. If they are, indeed, representatives of *T. soutoni*, they extend the geographic range of the species from Pondoland through Zululand and Mozambique to Madagascar.

Judging by similarities in ontogeny, *T. soutoni* s.s. can be derived from *T. umzambiense* sp. nov. or *T. presoutoni* s.s. sp. nov. (Figs 152–153). Unfortunately stratigraphic data are insufficient for determining the exact phylogenetic sequence, but it is assumed here that *T. soutoni* was probably derived from *T. umzambiense* via *T. presoutoni*. Differences between *T. soutoni* s.s. and *T. presoutoni* sp. nov. s.s. are gradational, being mainly a question of umbilical width and frequency of bifurcations on the phragmocone as noted above (p. 177). Specimens such as SAM-PCP5713 (Fig. 152B) or SAM-13090 (Fig. 160) with robust ornament consisting predominantly of single ribs on the phragmocone, are to be considered transitional between the two species. Similarly, the upper boundary between *T. soutoni* s.s. and *Submortonicer* *woodsii* is also gradational. Specimens with umbilical diameters in the vicinity of 35 per cent and greatly attenuated ornament on the phragmocone are best referred to *Submortonicer*, rather than *T. soutoni*.

The Zululand counterpart of *T. soutoni soutoni*, *T. soutoni natalense* ssp. nov., differs mainly in often having attenuated ornament on the inner whorls, a generally stouter whorl section and wider and shallower lobes, but is just as variable and grades laterally into the Pondoland subspecies.

In view of the extreme variation, comparisons with species outside southern Africa become tenuous.

*T. hourcqi* Collignon from the Middle Santonian of Madagascar is similar to the more evolute forms of *T. soutoni* s.s., but is more compressed. When compared with *T. soutoni* s.s. doubt arises if the possession of regularly bifurcating ribbing in *T. hourcqi* is as important a characteristic as implied by Collignon (1948: 79).

Young (1963: 90) erected a new species, *T. lonsdalei*, on the basis of one specimen and a questionable specimen, and included Collignon's (1948: 78, pl. 9(3) (fig. 1–1a)) *Texanites* cf. *soutoni* in the synonymy of that species. As interpreted here, Collignon's specimen may easily be accommodated in the variation of *T. soutoni* s.s., but not *T. lonsdalei* because of the much higher than





Fig. 159. *Texanites* sp. aff. *soutoni* (Baily, 1855). TM1439, from an unknown locality in Mozambique.  $\times 1$ .

wide whorl section (see especially Young, pl. 51 (fig. 5)). Young (1963: 91), however, paid more attention to similarities of ornament, and admitted that the Texan specimen 'may be crushed'. Even if the Texas specimen is crushed, the umbilical width is predominantly of the order of 32 to 35 per cent, with only one recording at 41,5 per cent. This places the species closer to *Submortonicer* *woods*, and Young (1963: 92) did, indeed, refer to this species (together with Woods's specimen of *Mortonicer* *soutoni* (1906, pl. 43 (fig. 1)) and *T. roemeri* as being 'close to the *Submortonicer*-*Texanites* taxonomic boundary' (Young



Fig. 160. *Texanites soutoni soutoni* (Baily, 1855). SAM-13090, a specimen transitional between *T. soutoni soutoni* and *T. presoutoni presoutoni* sp. nov.  $\times 0,65$ .



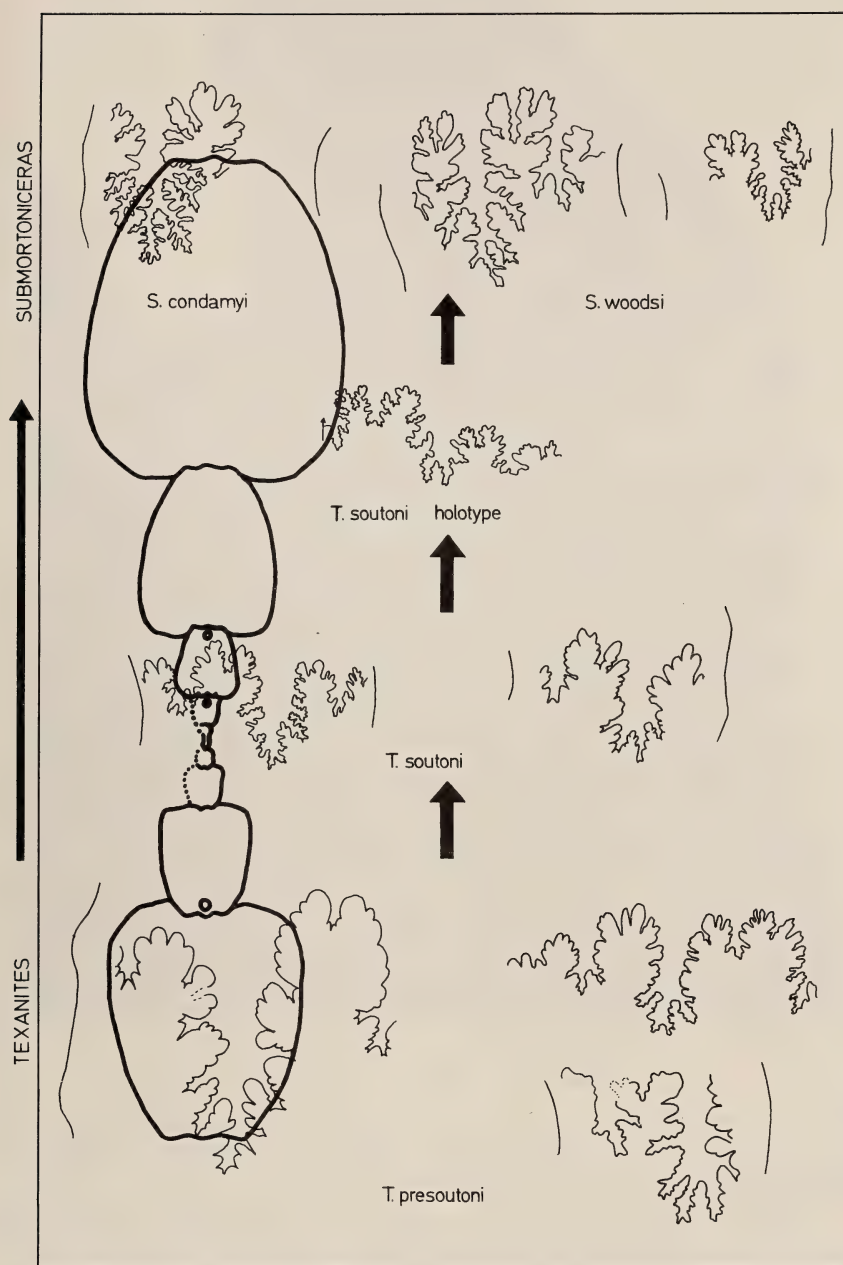


Fig. 161. Diagram illustrating apparent trend in suture line towards higher degree of complexity in development from *Texanites* to *Submorticeras*. Whorl section of *Texanites soutoni soutoni* superimposed.





Fig. 162. *Texanites soutoni soutoni* (Baily, 1855). BMNH-C19461.  
(British Museum photograph.)  $\times 0,95$ .

1963: 92). Until the question of the true whorl section of *T. lonsdalei* is resolved, the species has to be maintained with some doubt, but bearing in mind the affinity with the *T. soutoni*-*S. woodsi* plexus.

Detailed studies of the ontogeny of the species as outlined here (p. 194) definitely allay Matsumoto's suspicion (1970: 279) that *T. soutoni* could possibly have *Plesiotechanites* inner whorls.

#### Occurrence

*T. soutoni* s.s. is relatively common in the Upper Santonian of the Umzamba



Fig. 163. *Texanites soutoni soutoni* (Baily, 1855).  
BMNH-C19461. (British Museum photograph.)  $\times 0,95$ .

Formation of Pondoland at the type section, locality 1, and is also known from borehole and other subsurface material near Richards Bay, Zululand (Klinger & Kennedy 1977). Rare occurrences are known from Umkwelane Hill and the False Bay area of Zululand.

The species is very rare in Madagascar (Collignon 1948: 78), and as yet no good specimens have been figured from that area. In view of the other close similarities between Pondoland and Madagascar faunas, e.g. pseudoschloenbachiids, *Hauericeras*, etc., this is very surprising.

*Texanites soutoni* (Baily) *natalense* ssp. nov.

Figs 164–185

*Mortonicerias* sp. aff. *soutoni* Spath, 1921: 235.*Texanites soutoni* (Baily): Kennedy & Klinger, 1972: pls 72–73.*Etymology*

Refers to the geographic occurrence.

*Holotype*

SAS-H126B/3 (Figs 164–165), Bed B locality 105, south-eastern shores of False Bay, Zululand, St Lucia Formation, Late Santonian.

*Material*

Paratypes are SAS-H126/1, H126/2, H126A?/11, H126B/1, H126B/2, H126B/3a, H126E/1, H127B/1, Z1144–Z1147, Z1822, Z1869–Z1871, Z1881, Z1952, Z1952A–E, Z2054, Z2058, Z2199, SAM-PCZ5884, PCZ5886, all from locality 105, south-eastern shores of False Bay, Zululand, St Lucia Formation, Santonian III to Campanian I; and SAM-5492, and SAS-Z353 from an unknown locality near Umkwelane Hill, probably locality 14, St Lucia Formation, Santonian to Campanian. The letter after specimens with catalogue numbers beginning with H126 denotes the horizon at locality 105 (see Fig. 130).

*Dimensions*

|          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb: Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|------------|------------|---------------|-------------|-------------|-------------|
| H126E/1  | 91,0     | 29,0(31,9) | 37,0(40,4) | 0,78          | 31,5(34,6)  | 23          | 37          |
| Z1146    | 92,7     | 30,3(32,7) | 39,9(43,0) | 0,76          | 27,6(29,7)  | 23          | 35          |
| Z1145    | 133,0    | 45,0(33,8) | 55,0(41,4) | 0,82          | 50,0(37,6)  | 19          | 31          |
| H126B/2  | 117,0    | 36,0(30,8) | 44,0(37,6) | 0,82          | 43,0(36,8)  | 13 × 2      | 26          |
| Z1952    | 145,0    | 45,0(31,0) | 57,0(39,3) | 0,79          | 55,0(37,9)  | 24          | 28          |
| Z1869    | 150,0    | 49,0(32,6) | 62,0(41,3) | 0,79          | 55,0(36,7)  | 13          | 27          |
| Z2054    | 153,5    | 43,0(28,0) | 59,0(38,4) | 0,72          | 59,0(38,4)  | 24          | 33          |
| Z1952B   | 180,0    | 57,0(31,7) | 67,0(37,2) | 0,85          | 69,0(38,3)  | 13 × 2      | 30          |
| Z1844 at | 180,0    | 52,0(28,9) | 67,0(37,2) | 0,78          | 68,0(37,8)  | 15 × 2      | 30          |
| at       | 76,0     | 26,5(34,9) | 34,0(44,7) | 0,78          | 27,5(36,2)  | 14          | 36          |
| Z1870    | 180,0    | 62,0(34,4) | 70,0(38,9) | 0,89          | 71,0(39,4)  | 24          | 26          |
| H126B/3  | 187,0    | 56,0(29,9) | 73,0(39,0) | 0,77          | 69,0(36,9)  | 18          | 28          |
| Z2199    | 205,0    | 58,0(28,3) | 75,5(26,8) | 0,77          | 83,0(40,5)  | 30          | 30          |
| Z1822    | 261,0    | 75,0(28,7) | 94,0(36,0) | 0,79          | 101,0(38,7) | 22          | 24          |
| PCZ5884  | 263,0    | 76,0(28,9) | 97,0(36,9) | 0,78          | 97,0(36,9)  | —           | —           |
| Z1881    | 230,0    | 62,0(26,9) | 79,0(34,3) | 0,78          | 88,0(38,3)  | 29          | —           |
| Z353     | 236,0    | 63,0(26,7) | 90,0(38,1) | 0,70          | 90,0(38,0)  | 26          | 38          |

*Diagnosis*

Extremely variable, but basically moderately involute, with umbilical diameter of about 35 to 40 per cent in the adult stage, in juvenile specimens less. Whorl section higher than wide, with maximum costal width at the lateral (2) tubercle, or, infrequently in juvenile specimens, at umbilical edge. Umbilical wall varies from rounded to near-vertical to overhanging. Ornament varies





Fig. 164. *Texanites soutoni natalense* ssp. nov. Holotype SAS-H126B/3.  $\times 0,75$ .

from weak to strong. Some specimens tend to develop a smooth *Submortoniceras*-like ornament on the inner phragmocone whorls, followed by normal *Texanites* ornament on the outer phragmocone whorls. The umbilical (1) tubercles point inward, the lateral (2) tubercles are clavate on the inner whorls, but tend to become radially elongated on the outer whorls, and may be very prominent. The submarginal, marginal and external (3–5) tubercles are clavate throughout. Ribs on body chamber may curve slightly forward over the flanks, with oblique, prorsiradiate extensions over the umbilical wall. Bifurcations and



Fig. 165. *Texanites soutoni natalense* ssp. nov. Holotype SAS-H126B/3.  $\times 0,9$ .





Fig. 166. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z2199.  $\times 0,67$ .

intercalations occur frequently on the inner whorls, but become scarcer on the outer whorls. Suture is of the normal collignoniceratid pattern, but with wide, open lateral lobe (L) and  $U_2$ , tending to become minutely frilled in some specimens (Fig. 185).

#### *Description*

Texanitids occur abundantly along the south-eastern shores of False Bay, Zululand, at locality 105, a steep cliff-face approximately 10 m high (see p. 173,



Fig. 130). A few specimens from Umkwelane Hill are also conspecific with this assemblage.

The material is extremely variable and hardly two specimens are alike. Differences are restricted mainly to strength of ornament at comparable diameters, and relative proportions. For descriptive purposes, three morphological varieties may be recognized: a typical form, an inflated form, and a compressed form. Differences between these three varieties may be slight and boundaries gradational, and, lacking precise stratigraphic control, are probably predominantly isochronous. In lieu of long descriptions the extent of variation will be illustrated as far as possible.

### *Forma typica*

Apart from the holotype, SAS-H126B/3 (Figs 164–165), specimens to be referred to the typical form are SAS-Z2199 (Figs 166–167A), SAS-H126B/1, SAS-H126B/2 (Fig. 168), SAS-H126B/3a (Fig. 169), SAS-Z1952 (Figs 170–171), SAS-Z1144 (Fig. 172) and SAM-5492 (Fig. 173). These specimens all have inner whorls with weaker ornament than the outer whorls, but details differ considerably. Thus SAS-H126B/3a (Fig. 169) has relatively coarser and more prominent ornament on the inner whorls at comparable diameters than the holotype, SAS-H126B/3 or SAS-H126B/2, even though they all occur within the same horizon at locality 105. SAS-Z1144 differs from the rest of the specimens in having abundant weak, bifurcating ribs on the inner whorls. One fragment, with part of the body chamber preserved, SAS-H126/2 (Fig. 174), with weakened but still visible ornament, may possibly belong to the typical form. None of the specimens has the complete body chamber preserved.

### *Var. inflata*

Specimen SAS-Z1870 (Figs 175–176), and to a lesser extent SAS-Z1822 (Figs 177–178) differ from the rest of the material in being much more inflated and in having a smaller umbilical diameter, and may be referred to as var. *inflata*. This variety also differs from the typical form in lacking smooth or weaker ornamented inner whorls. Tuberculation here persists on part of the body chamber preserved in SAS-Z1879 (Fig. 175). Transitions to the typical form occur via SAS-H126B/2 (Fig. 168).

### *Var. compressa*

Two specimens, SAS-Z1881 (Figs 179–180B) and SAS-Z353, differ from the others in being more laterally compressed and in having weaker ornament throughout, and may be referred to as var. *compressa*. As far as preservation permits examination, a smooth inner stage appears not to be present.

### *Juvenile specimens*

A number of juvenile specimens, SAS-Z1146–Z1147, SAS-Z1871, SAS-Z1952E, SAS-H126E/1, SAS-H127B/1, and SAM-PCZ5886, and, possibly,



Fig. 167. A. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z2199.  $\times 0,76$ . B. *Texanites presoutoni natalense* ssp. nov. Paratype SAM-PCZ5885.  $\times 0,72$ .

NMB-D1320 are also referable to this species plexus, although positive reference to any of the above varieties is not possible. Variation in respect of strength of ornament and whorl section is as considerable as in the adult population. Specimens SAS-H127B/1 (Fig. 183B) and SAS-H126E/1 (Fig. 181B) suggest that the specimens with more compressed *Submortonicer*-like whorls occur higher up in the sequence than those with more inflated whorl sections. Two sets of specimens with similar relative proportions at equal diameters, SAS-Z1146-Z1147, SAS-Z1871, SAS-H126E/1, and SAS-Z1952E, SAS-H127E/1, SAM-PCZ 5886 respectively, again illustrate the variation in strength of ornament (Figs 181-183), NMB-D1320 is more inflated than any of the other juvenile specimens, and may possibly belong to another species.



Fig. 168. *Texanites soutoni natalense* ssp. nov. Paratype SAS-H126B/2. Typical form.  
× 0,89.



*Interrelationships of varieties*

The majority of specimens in the present collection belong to the typical form, whereas the other two varieties are poorly represented. Due to lack of sufficient stratigraphic data, the temporal relationship of the different varieties is not very clear. We know only that the typical *Submortonicer* forms are youngest, and that those forms with smooth *Submortonicer*-like inner whorls



Fig. 169. *Texanites soutoni natalense* ssp. nov. Paratype SAS-H126B/3a. Typical form.  $\times 0,82$ .



Fig. 170. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1952. Typical form.  $\times 1$ .

first occur in Bed B at locality 105. Suggested lines of development are outlined in Figure 132.

*Submortoniceras woodsi natalense* ssp. nov. may be derived proterogenetically from *T. soutoni natalense forma typica*; the inner smooth stage is retained for progressively longer periods of growth, accompanied by a simultaneous reduction of umbilical width and compression. Var. *inflata* appears to be sterile. As in *T. soutoni soutoni*, it seems possible to derive a widely umbilicate,



Fig. 171. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1952. Typical form.  $\times 1$ .



compressed submortoniceratine form such as SAS-Z1762 (Fig. 184) from var. *compressa*. As in the nominate subspecies, this compressed lineage also seems to be a dead-end.

### Discussion

This subspecies is very variable, and should be interpreted in terms of consanguinity of characteristics predominating in the majority of specimens rather than narrowly defined characteristics present only in the holotype.

The stratigraphic occurrence of typical specimens in Bed B at locality 105 (Fig. 130), immediately overlying Bed A containing *T. presoutoni natalense*, may suggest genetic relationship between the two species, as here assumed (Fig. 132). Similarly, the relatively higher stratigraphic occurrence of *Submortoniceratas woodsi natalense* again seems to support genetic relationship between the two.

*T. soutoni natalense* ssp. nov. is of age similar to the predominantly Pondoland subspecies *T. soutoni* s.s. It is associated with an ammonoid fauna consisting of *Hauericeras gardeni*, *Pseudoschloenbachia umbulazi* and varieties, 'Heteroceras' *amapondense* and *Pseudophyllites latus* (Fig. 130), similar to that of Umzamba Cliff (Klinger & Kennedy in press) but in much reduced numbers. Coarsely ornamented forms lacking the inner whorls, as SAS-Z1952 (Fig. 170), are indistinguishable from inflated forms of *T. soutoni* s.s. Current evidence seems to suggest that *T. soutoni* s.s. flourished in the shallow water of the transgressive sequence ranging from Umkwelane Hill in the north to Pondoland in the south, whereas *T. soutoni natalense* inhabited the deeper part of the sedimentary basin in the False Bay area. Intermingling took place in the vicinity of Umkwelane Hill. In this regard *T. soutoni soutoni* and *T. soutoni natalense* may qualify for subspecific status in the biological sense.

Major differences between *T. soutoni soutoni* and *T. soutoni natalense* are: the presence of a relatively smooth *Submortoniceratas*-like stage on the inner whorls of some specimens, followed by more coarsely ornamented *Texanites*-like ornament on the outer whorls; generally smaller size and the presence of a wide, shallow lateral and umbilical lobe; and more inflated whorl section in *T. soutoni natalense*.

The juvenile specimens described above (Figs 181–183), may be compared with a number of figured texanitid species, but specific differentiation at these diameters is impossible, e.g.:

*Submortoniceratas woodsi* (Spath) (see below).

*Submortoniceratas tequesquitense* Young (see especially Young 1963, pl. 51 (fig. 1), pl. 28 (fig. 1)).

*Texanites texanus gallica* (in Young 1963, especially pl. 38 (fig. 3)).

*Texanites hourcqi* Collignon (Collignon 1948, pl. 7(1) (fig. 1)) etc.

The adult stages of these species, however, usually reveal the differences with *T. soutoni natalense*.



Fig. 172. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1144. Typical form.  $\times 0,89$ .



Fig. 173. *Texanites soutoni natalense* ssp. nov. Paratype SAM-5492. Typical form. This is the specimen described by Spath (1921: 235) as *Mortoniceras* sp. aff. *soutoni*.  $\times 1$ .





Fig. 174. *Texanites soutoni natalense* ssp. nov. Paratype SAS-H126/1. Specimen with part of the body chamber preserved; probably belonging to the typical form. Note continuation of pentatuberculate ornament on body chamber section.  $\times 0,57$ .

SAS-Z1881 (Fig. 179), here named var. *compressa*, is remarkably similar to the holotype of *Texanites shiloensis* (see Young 1963, pl. 46 (fig. 1)) in having a more or less *Submortonicer*-like ornament on the outer whorl. As shown below, relative proportions are similar.

*Dimensions*

|                          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|--------------------------|----------|------------|------------|------------|-------------|-------------|
| UT-1986                  | 275,0    | —          | (32,0)     | (40,0)     | 31          | 31          |
| ( <i>T. shiloensis</i> ) |          |            |            |            |             |             |
| Z1881                    | 230,0    | 62,0(26,9) | 79,0(34,3) | 88,0(38,3) | 30          | —           |



Fig. 175. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1870. Variety *inflata*.  $\times 0,68$ .



Fig. 176. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1870. Variety *inflata*.  $\times 0,68$ .



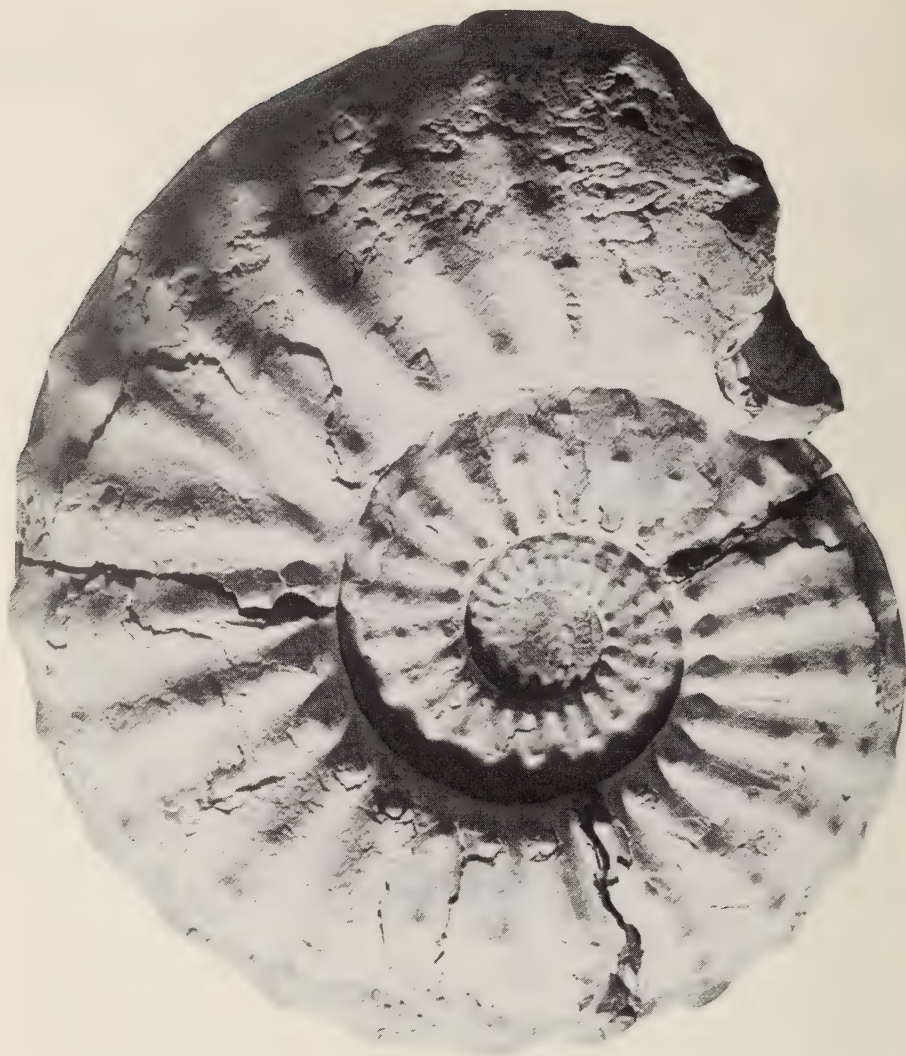


Fig. 177. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1822. Variety *inflata*.  $\times 0,52$ .

The holotype of *T. shiloensis* has a measured diameter of 275 mm, and the only apparent difference between the two, apart from size, is the finer, denser ribbing with frequent intercalations on the inner whorls. In addition to being very similar to the present material, *T. shiloensis* is of further interest in that it grades vertically into *Submortonicerias tequesquitense*. As far as relative size is concerned, *T. shiloensis* is close to the compressed variety of *T. soutoni* s.s., e.g. specimen SAM-7077 (Fig. 146), but in the weakened ornament is closer to *T. soutoni natalense*, e.g. SAS-Z1881 (Fig. 179).

Given sufficient material, it may eventually prove possible to refer *T. shiloensis* and *S. tequesquitense* to the group of *T. soutoni*–*S. woodsi* at subspecific level, as a North American population.

#### Occurrence

Upper Santonian of Zululand.

Genus *Submortonicer*as Spath, 1921

(= *Butticeras* Anderson, 1958

?= *Jimenesites* Carrasco, 1967

?= *Antsirasiarella* Collignon, 1966

?= *Ankilizatella* Collignon, 1970)

#### Type species

*Mortonicer*as *woodsi* Spath, 1921, by original designation of Spath.

#### Diagnosis

Coiling generally involute, with whorls increasing rapidly in size. Pentatuberculate from a relatively early stage, but there is a distinct tendency towards loss of lateral ornament on the outer whorls. Whorl section generally compressed, especially in the later species.

#### Discussion

Intraspecific variation in *Submortonicer*as species is bewildering, even by *Texanites* standards as applied in the South African material. The large number of seemingly endemic species probably results from the difficulty encountered in trying to compare species from different areas.

The species below are those referred to *Submortonicer*as in the literature. A great number of these are probably synonymous, as will be discussed below.

*S. angustumbilicatum* Collignon (1948: 105, pl. 16 (figs 1–1b, 2–2a)) from the Middle Campanian of Madagascar.

*S. behamotrense* Collignon (1970: 46, pl. 626 (figs 2318–2320)) from the Middle Campanian of Madagascar.

*S. candelariae* Young (1963: 102, pl. 56 (figs 1, 3–4), pl. 60 (fig. 8), text-figs 20b, 28af, 29ae, 34af) from the Lower Campanian of the Gulf Coast of North America.

*S. chicoense* (Trask) (1856: 92, pl. 2 (fig. 1)) from the Lower Campanian of California, Texas, and James Ross Island Group.

*S. collignoni* Shimizu, 1935 (= *M. woodsi* in Collignon 1932: 35, pl. 5 (fig. 2–2b) text-fig. 19) from the Middle Campanian of Madagascar.

*S. condamyi* Collignon (1932: 36, pl. 5 (fig. 3–3b), text-fig. 20) from the Lower Campanian of Madagascar and South Africa.

*S. debile* Collignon (1948: 103, pl. 19(13) (fig. 3–3a)) from the Middle Campanian of Madagascar.

*S. dubium* Collignon (1948: 97, pl. 18(12) (fig. 3–3b)) from the Middle Campanian of Madagascar.

- S. elimatum* Collignon (1948: 104, pl. 20(14) (fig. 2-2a)) from the Lower Campanian of Madagascar.
- S. franiattae* Collignon (1970: 43, pl. 626 (fig. 2316)) from the Middle Campanian of Madagascar.
- S. imlayi* Collignon (1948: 101, pl. 20(16) (fig. 3-3a)) from the Middle Campanian of Madagascar.
- S. johannisludovici* Collignon (1970: 47, pl. 628 (fig. 2321)) from the Middle Campanian of Madagascar.
- S. mariscalense* Young (1963: 104, pl. 59 (fig. 3), pl. 60 (figs 1, 4-6), text-fig. 14bf) from the Lower Campanian of the Gulf Coast of North America.
- S. pauper* Collignon (1948: 103, pl. 18 (fig. 2-2a)) from the Lower and Middle Campanian of Madagascar.
- S. pivetequi* Collignon (1948: 102, pl. 7(1) (fig. 6-6b), pl. 19(13) (fig. 2-2a)) from the Middle Campanian of Madagascar.
- S. punctatum* Collignon (1948: 99, pl. 18(12) (fig. 1-1a)) from the Lower Campanian of Madagascar.
- S. rarecostum* Collignon (1948: 101, pl. 20(14) (fig. 3-3a)) from the Middle Campanian of Madagascar.
- S. renniei* Collignon (1948: 106, pl. 17 (fig. 1)) from the Lower Campanian of Madagascar.
- S. rugetae* Collignon (1969: 189, pl. 593 (fig. 2242)) from the Lower Campanian of Madagascar.
- S. sancarlosense* Young (1963: 100, pl. 55 (figs 1-4), pl. 62 (fig. 3), text-figs 20g, 27d) from the Lower Campanian of the Gulf Coast of North America.
- S. spathi* Collignon (1948: 106, pl. 20(14) (fig. 1-1a)) from the Middle Campanian of Madagascar.
- S. tenuicostulatum* Collignon (1948: 96, pl. 19(13) (fig. 1-1b)) from the Lower and Middle Campanian of Madagascar.
- S. tequesquitense* Young (1963: 97, pl. 28 (fig. 1), pl. 42 (figs 1-2), pl. 44 (figs 4-5), pl. 51 (figs 1-2), pl. 52 (figs 1-4), pl. 57 (fig. 4), pl. 70 (fig. 1), text-figs 12b, 28b) from the Lower Campanian of the Gulf Coast of North America.
- S. uddeni* Young (1963: 105, pl. 59 (figs 1-2, 4-9), pl. 60 (figs 2-3, 7, 9-10), text-figs 14de, 28c) from the Lower Campanian of the Gulf Coast of North America.
- S. vanuxemi* (Morton) (1830: 244, pl. 3 (figs 3-4)) from the Campanian of North America.
- S. vandaliaense* Young (1963: 102, pl. 55 (figs 6-7), text-fig. 26a) from the Lower Campanian of the Gulf Coast of North America.
- S. woodsi* (Spath) (1921: 223, pl. 21 (fig. 1a-d)) from the Lower Campanian of Madagascar and South Africa.
- '*Butticeras*' *buttense* Anderson (1958: 272, pl. 53 (figs 3-4)) from the Lower Campanian of the Pacific Coast of America.
- '*Butticeras*' *studleyi* Anderson (1958: 272, pl. 51 (figs 3-4)) from the Lower Campanian of the Pacific Coast of America.





Fig. 178. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1822. Variety *inflata*.  $\times 0,6$ .



Fig. 179. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1881. Variety *compressa*.  
× 0,59.

Anderson (1958: 272) introduced the genus *Butticeras*, with type species *Butticeras buttense*, for a group of small ammonites in which the keel is lost in maturity, the venter becomes rounded, and all lateral tuberculation is lost except the umbilical and external rows. Matsumoto (1959: 132) speculated that *Butticeras* may represent an extreme form of *Submortonicer* *chicoense*, though not definitely committing himself. Consequently, *Butticeras* should be regarded as a junior synonym of *Submortonicer*. This appears to be reasonable procedure, as subdivision of such a variable genus should be limited to the absolute

minimum. On this basis it would also be advisable to include the monotypical subgenus *S. (Antsirasiarella)* Collignon (type species *S. (Antsirasiarella) stellata* Collignon (1969: 201, pl. 599 (fig. 2252)) in the strict synonymy of *Submortonicer*as. *S. (Antsirasiarella) stellata* has extremely reduced lateral ornament, similar to *Butticeras*, but has a flattened venter in the adult stage, thus differing from the latter. For the present it is probably best to consider *S. (Antsirasiarella)* as merely representing an extreme development of the attenuation of ornament in *Submortonicer*as.

The monospecific subgenus *Texanites* (*Ankilizatella*) Collignon (type species *T. (Ankilizatella) ankilizatensis* Collignon 1970: 50–51, pl. 629 (figs 2322–2325)) from the Middle Campanian of Madagascar is probably better placed in *Submortonicer*as than in *Texanites*. The type (and only) species has a compressed disc shape and smooth outer whorls as in *Submortonicer*as, but a wide umbilicus as in *Texanites*. The compressed section and lack of ornament on the outer whorls are more characteristic of *Submortonicer*as than of *Texanites*. As far as umbilical width is concerned, *Ankilizatella* possibly connects with *Submortonicer*as s.s. via *S. behamotrense*, *S. renniei* and *S. mariscalense*; especially the former.

*Submortonicer*as is easily distinguished from most texanitine genera by virtue of the generally tight coiling and attenuation of ornament on the outer whorls. Difficulties arise, however, in the Middle Campanian in distinguishing between *Submortonicer*as and *Menabites* (*Delawarella*), especially when the inner whorls are lacking. Matsumoto (1959: 125–6) preferred to refer *M. (Delawarella)* as a subgenus to *Submortonicer*as rather than to *Menabites*, but later (Matsumoto 1970: 299) retracted this view. From a phylogenetic point of view, however, this former procedure cannot be accepted (see also Young 1963: 39). *M. (Delawarella)* typically has a multiplied row of external tubercles, characteristic of *Menabites* s.l., and is often trituberculate to a large diameter. However, when lateral ornament is attenuated, it is difficult to see whether the greater number of external tubercles is due to the original multiplication of *Menabites* s.l., or due to abundant bifurcations and intercalations of *Submortonicer*as. Young's (1963: 76) key to the classification of the Texanitinae is of little use in this case. Despite this example of isochronous homoeomorphy, *Submortonicer*as and *Delawarella* should be maintained separate, because of different phylogenies and ontogenetic development.

Both Young (1963: 39) and Matsumoto (1970: 239) agree in deriving *Submortonicer*as from *Texanites*, a view corroborated by the South African material. As described above, *S. woodsi* is derived gradually from *T. soutoni* through reduction of umbilical diameter and effacement of the ornament on the outer whorls. *Submortonicer*as appears to be a dead-end in texanitine development, and the last *Submortonicer*as species occur in the Middle Campanian of Madagascar.

As is seen from the list of species referred to the genus, the majority seem to be endemic to the regions from which they were first described. None of the





Fig. 180. *Texanites soutoni natalense* ssp. nov. A. Paratype SAS-Z1144. Typical form.  $\times 0,6$ . B. Paratype SAS-Z1881. Var. *compressa*.  $\times 0,69$ .

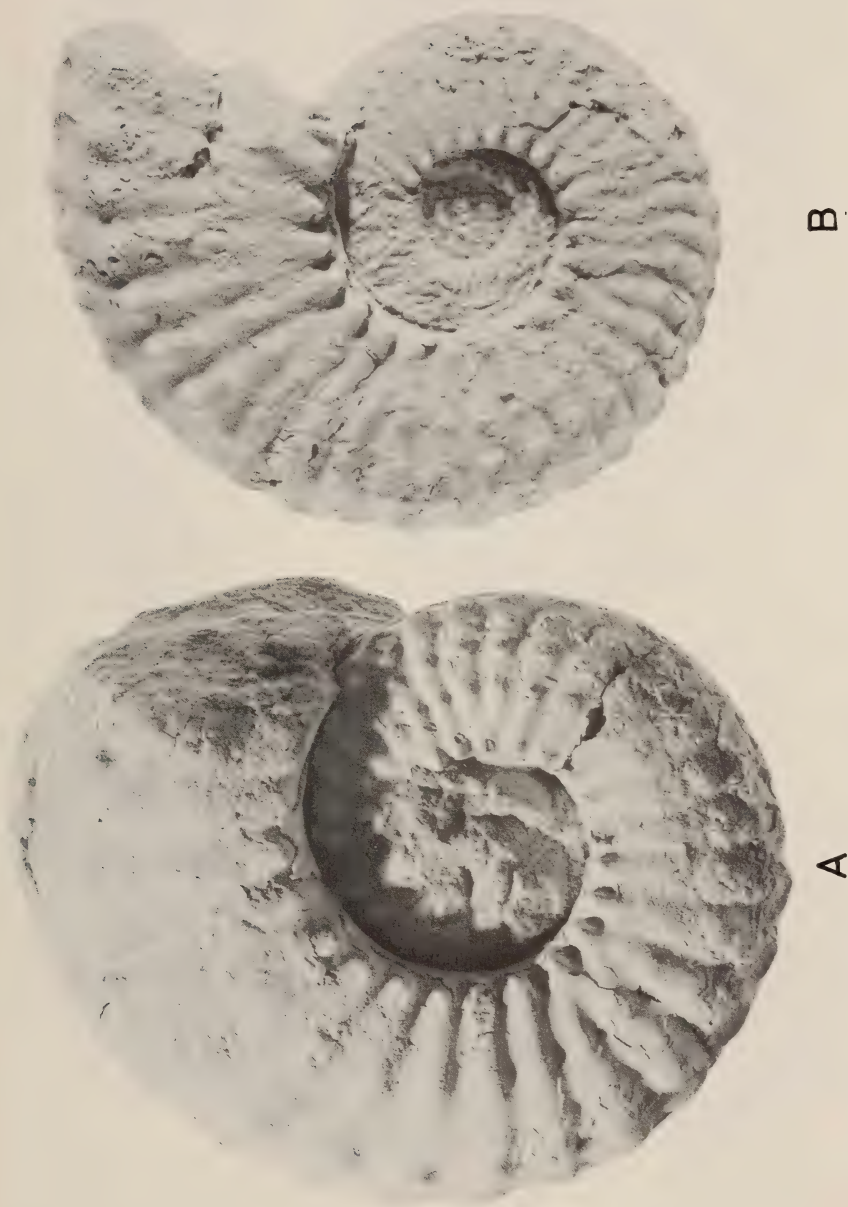


Fig. 181. *Texanites soutoni natalense* ssp. nov. Juvenile paratypes. A. Z1147. B. SAS-H126E/1.  $\times 1$ .

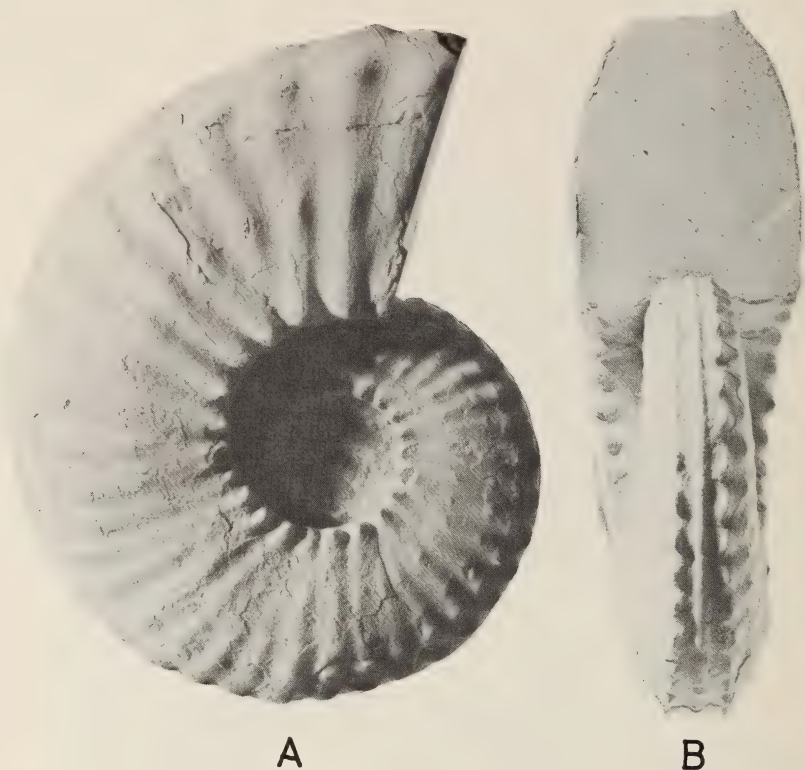


Fig. 182. *Texanites soutoni natalense* ssp. nov. Juvenile paratype SAS-Z1146 with much attenuated ornament.  $\times 1$ .

species described from Madagascar is known to occur definitely in North America and vice versa. This causes one to think that *Submortonicer* is either restricted to certain geographic areas with little or no intermingling between the populations, but highly successful and populous as far as number of species are concerned, or it is an extremely successful group with limited speciation potential but wide dispersion and tremendous intraspecific variation. Analysis of the South African material and work by Matsumoto (1959) seem to suggest the latter. In his examination of *S. chicoense*, Matsumoto (1959) was able to recognize three morphological variants, *forma*  $\alpha$ ,  $\beta$  and  $\gamma$ , which, by traditional systematic procedure, would probably qualify for separate specific rank. He found, however, that there was a continuous gradation from one form to the other, and that the different types may even occur in the same nodule. In addition, Matsumoto tentatively compared the Californian specimens with some of the numerous species of *Submortonicer* described by Collignon (1948) from Berere, Madagascar. *S. piveteaui* resembles *S. chicoense forma*  $\alpha$ , *S. imlayi* is close to *forma*  $\beta$ , and *S. angusteumbilicatum* and *S. spathi* are close





Fig. 183. *Texanites soutoni natalense* ssp. nov. Juvenile paratypes. A. SAM-PCZ5886. B. SAS-H126B/1. C. SAS-Z1952.  $\times 1$ .



Fig. 184. *Texanites soutoni natalense* ssp. nov. Paratype SAS-Z1762. Compressed, widely umbilicate variety probably derived from var. *compressa* (see also Fig. 132).  $\times 0,48$ .

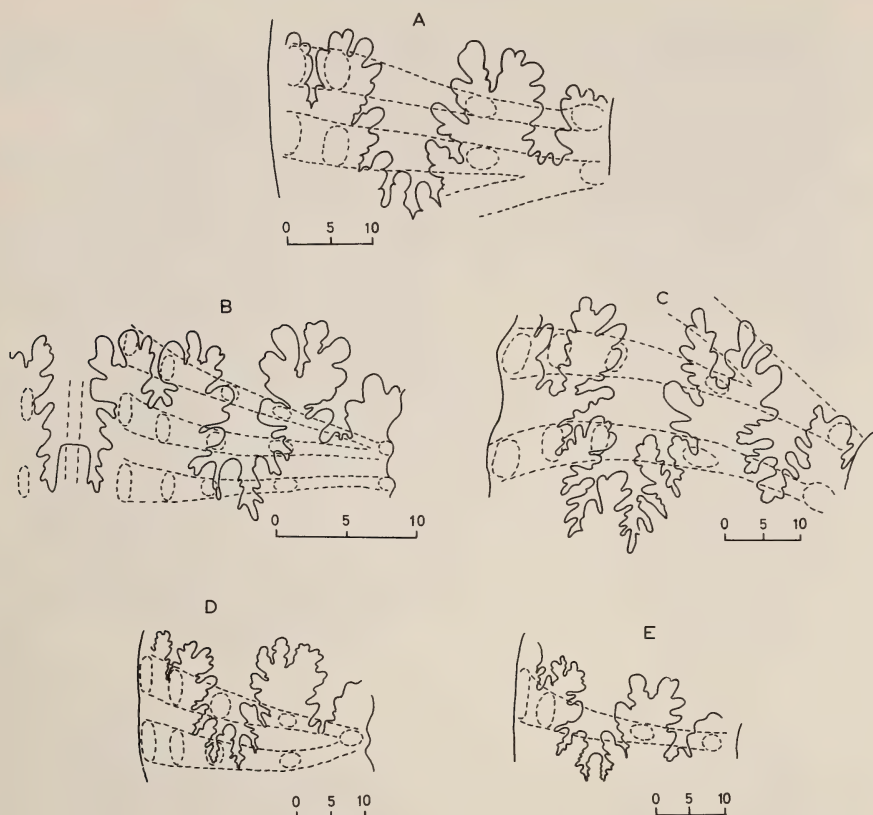


Fig. 185. *Texanites soutoni natalense* ssp. nov. Suture lines of paratypes. A. SAS-Z1881. B. SAS-Z1146. C. SAS-Z358. D. SAS-Z1871. E. SAS-Z1147.

to *forma*  $\gamma$  of *S. chicoense*. Even though Matsumoto would not definitely commit himself to synonymizing the species without having seen the Madagascar species in their stratigraphic context, it is gratifying to see that the 'endemic' gap between the North American and Madagascar species can be narrowed.

The South African material is as variable as *S. chicoense*, and is here referred to the two existing species *S. woodsi* and *S. condamyi*. As will be seen in the systematic descriptions below, ornament and suture are extremely variable. Specimens with smooth inner whorls occur at the same stratigraphic level as heavily ornamented ones, and are connected by transitions. In the South African material, ornament is partially associated with geographic location, suggesting that ornament alone is of very little systematic value in the classification of *Submortonicer* species. There appears to be a definite trend in the South African *Submortonicer* population towards progressive tighter coiling and compression of the whorls. At present the significance of this is not clear,



but the authors would suggest that it may be connected in some way to a slightly deeper water habitat or more active way of life. A similar trend is found in the Gulf Coast deposits of North America where *Texanites shiloensis* grades upward into *Submortonicerias tequesquitense* (see Young 1963: 90).

Consequently, degree of involution is here considered of maximum value in classifying *Submortonicerias* species.

This all suggests that the number of species listed above may be greatly reduced, provided sufficient detailed stratigraphic data and material become available.

### Occurrence

*Submortonicerias* species occur profusely in the Lower and Middle Campanian of Madagascar, and in slightly smaller numbers in the Upper Santonian–Lower Campanian of South Africa, the Lower Campanian of the Pacific Coast and Gulf Coast areas of North America, and sporadically in British Columbia. A single specimen of *S. chicoense* was reported from the Sub-Antarctic James Ross Island Group. Young (1963: 39) refers Redtenbacher's (1873) *Ammonites propoetidum* to the genus *Submortonicerias*, but the authors would rather place this species in *Gauthiericerias*, as was done by Reymont (1958), or in *Zuluicerias* Van Hoepen.

### *Submortonicerias woodsi* s.l. (Spath, 1921)

Figs 186–199, 200B

*Mortonicerias woodsi* Spath, 1921: 232, pl. 21 (fig. 1a–d). *Non* Besairie, 1930: 637, pl. 67 (fig. 1) (= *S. angusteumbilicatum* Collignon). ?*Non* Collignon, 1932: 35, pl. 5 (fig. 2–2b) (= *S. collignoni* Shimizu).

*Mortonicerias vanuxemi* (Morton): Spath, 1921: 308, pl. 23 (fig. 4a–4b).

*Submortonicerias woodsi* (Spath): Collignon, 1948: 43. Kennedy & Klinger, 1973: 103, pl. 2 (fig. 3), pl. 3 (figs 2–3), pl. 5 (fig. 3).

### Type

Holotype is SAM-5451 (Fig. 186) from an unknown horizon at Umkwelane Hill near Mtubatuba, Zululand, St Lucia Formation, Santonian to Campanian.

### Material

SAS-Z1875, Z1138, Z1893, SAM-PCZ5884, PCZ5883, all from locality 105, south-eastern shores of False Bay, St Lucia Formation, Upper Santonian to Lower Campanian; SAM-PCZ5896 and BMNH-C81489, from Umkwelane Hill, near locality 14, St Lucia Formation, Upper Santonian to Lower Campanian; SAM-PCZ5897, locality 6, Richards Bay, St Lucia Formation, Upper Santonian to Lower Campanian; SAM-PCP5716, Bed A3 locality 1, Umzamba Formation, Upper Santonian to Lower Campanian; BMNH-C81487, locality 74, Santonian III; and BMNH-C81488 from the same locality, St Lucia Formation, Campanian I.

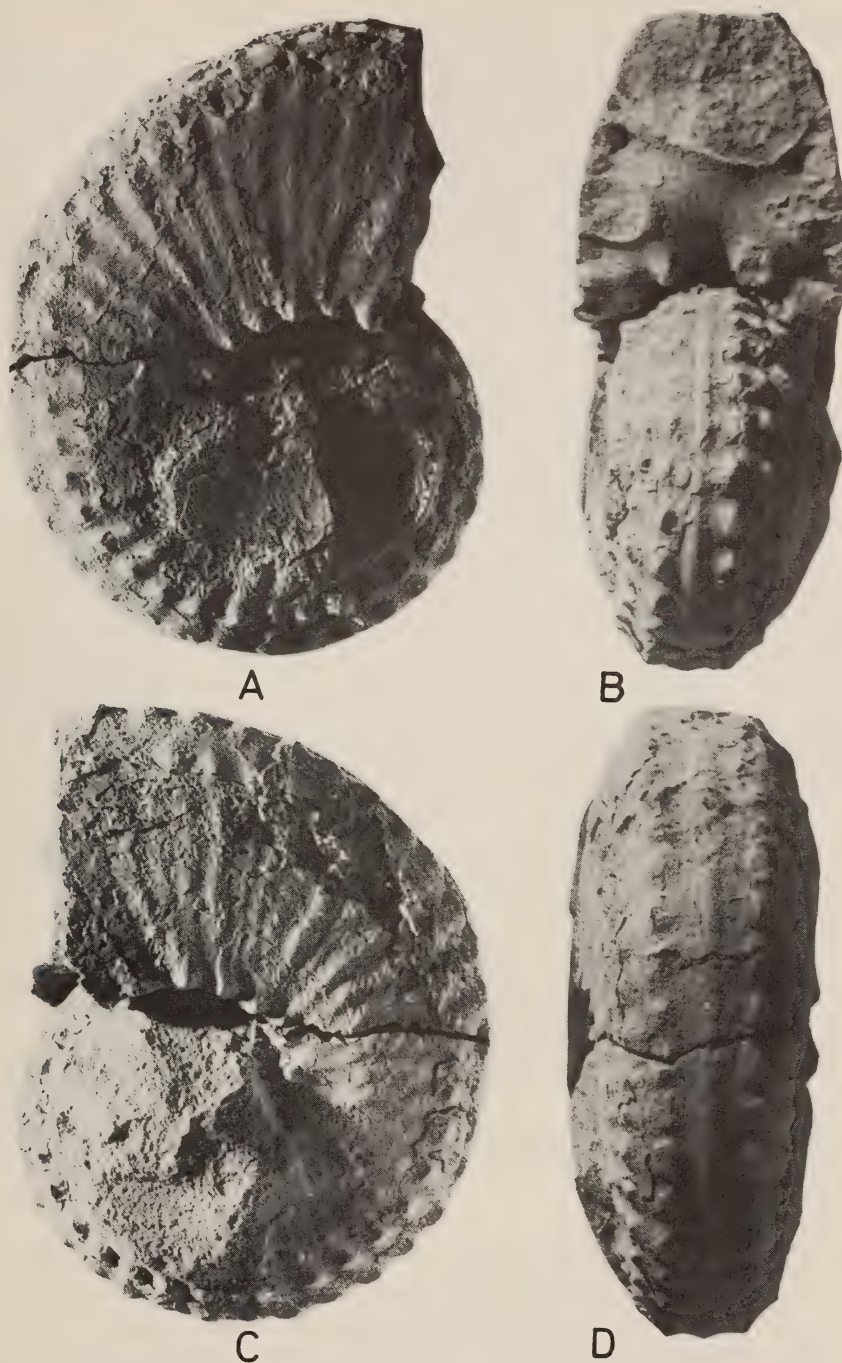


Fig. 186. *Submortonicerias woodsi woodsi*. Holotype SAM-5451.  $\times 1$ .

*Dimensions*

|          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>   | <i>Wb : Wh</i> | <i>U</i>    | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|------------|-------------|----------------|-------------|-------------|-------------|
| Holotype | 78,0     | 30,5(39,1) | 38,5(49,3)  | 0,79           | ?25%        | —           | 35          |
| Z1875    | 325,0    | —          | 115,0(35,4) | —              | —           | 29          | 30          |
| Z1138    | 294,0    | 80,0(27,2) | 105,0(35,7) | 0,76           | 115,0(39,1) | 31          | 35          |
| at       | 198,0    | 57,5(29,0) | 76,5(38,6)  | 0,75           | 69,0(34,9)  | 24          | 41          |
| PCZ5897  | 226,0    | 74,0(32,7) | 92,0(40,7)  | 0,80           | 74,0(32,7)  | 25          | 34          |
| PCZ5884  | 262,0    | 76,0(29,0) | 100,0(38,2) | 0,76           | 90,0(34,4)  | 25          | 30          |
| PCP5716  | 270,0    | 90,0(33,3) | 108,0(40,0) | 0,83           | 87,0(32,2)  | 28          | 37          |
| Z1893    | 280,0    | 84,0(30,0) | 108,0(38,7) | 0,78           | 102,0(36,5) | 25          | 34          |

*Diagnosis*

Species with umbilical width of the order of *c.* 35 per cent of total diameter. Ornament generally weakens from inside outwards on phragmocone, but specimens with virtually smooth inner whorls occur. In some specimens lateral ornament on body chamber is strong.

*Description*

Coiling is generally involute with an umbilical width of the order of *c.* 35 per cent of the total diameter, but may be as high as 39 per cent, connecting with *Texanites soutoni* s.l., as on the outer whorls of SAS-Z1138 (Fig. 187).

The whorl section is higher than wide throughout, with a steep to overhanging umbilical wall (Figs 197, 200B), weakly inflated flanks on the inner whorls, but more inflated on the late phragmocone and on the body chamber.

Ornament on the phragmocone varies considerably, from virtually smooth, barring slight radial striations indicative of weak ribbing in SAS-Z1875 (Figs 188–189) and SAS-Z1138 (Figs 187, 190), through weakly tuberculate as in SAM-PCZ5884 (Fig. 191), to coarsely ornamented in SAM-PCZ5897 (Fig. 192), SAS-Z1893, and SAM-PCP5716 (Fig. 193). All ornament, where present on the inner whorls, weakens toward the middle part of the phragmocone, but thereafter becomes stronger again towards the later part of the phragmocone and the body chamber. Very strong ribbing is developed in SAS-Z1138 (Fig. 187) on the body chamber, containing the full complement of pentatuberculate ornament. Lateral tuberculation is also still visible on the body chambers of SAS-Z1875 (Fig. 188), SAM-PCZ5896 and SAM-PCZ5897 (Fig. 192). SAM-PCP5716 (Fig. 193) has a few bifurcating ribs on the body chamber as in *Texanites soutoni* s.s.

The suture line is variable, ranging from wide, short lobes to long and narrowly played lobes (Figs 187, 190–194).

*Discussion*

The authors have previously commented on the difficulty in interpreting this species (Kennedy & Klinger 1973: 103). Spath's original figures are poor, his description is too brief and stratigraphic data are lacking.

The holotype of *Mortoniceras woodsi*, here refigured as Figure 186, is based on an incomplete inner whorl of a specimen *c.* 80 mm in diameter, from





Fig. 187. *Submorticeras woodsi natalense* ssp. nov. Paratype SAS-Z1138. Specimen with wide umbilicus, connecting to *Texanites soutoni*.  $\times 0,5$ .

an unknown horizon at Umkwelane Hill. The innermost whorls up to a diameter of *c.* 50 mm are incomplete, and only the ventral half of the flanks and the venter are preserved, showing strong marginal (4) and external (5) tubercles, weaker submarginal (3) tubercles, and an entire keel. The last third of a whorl preserved on the holotype shows very faint ribs bifurcating from strong inward leaning umbilical (1) tubercles, with very faint lateral (2) tubercles, slightly

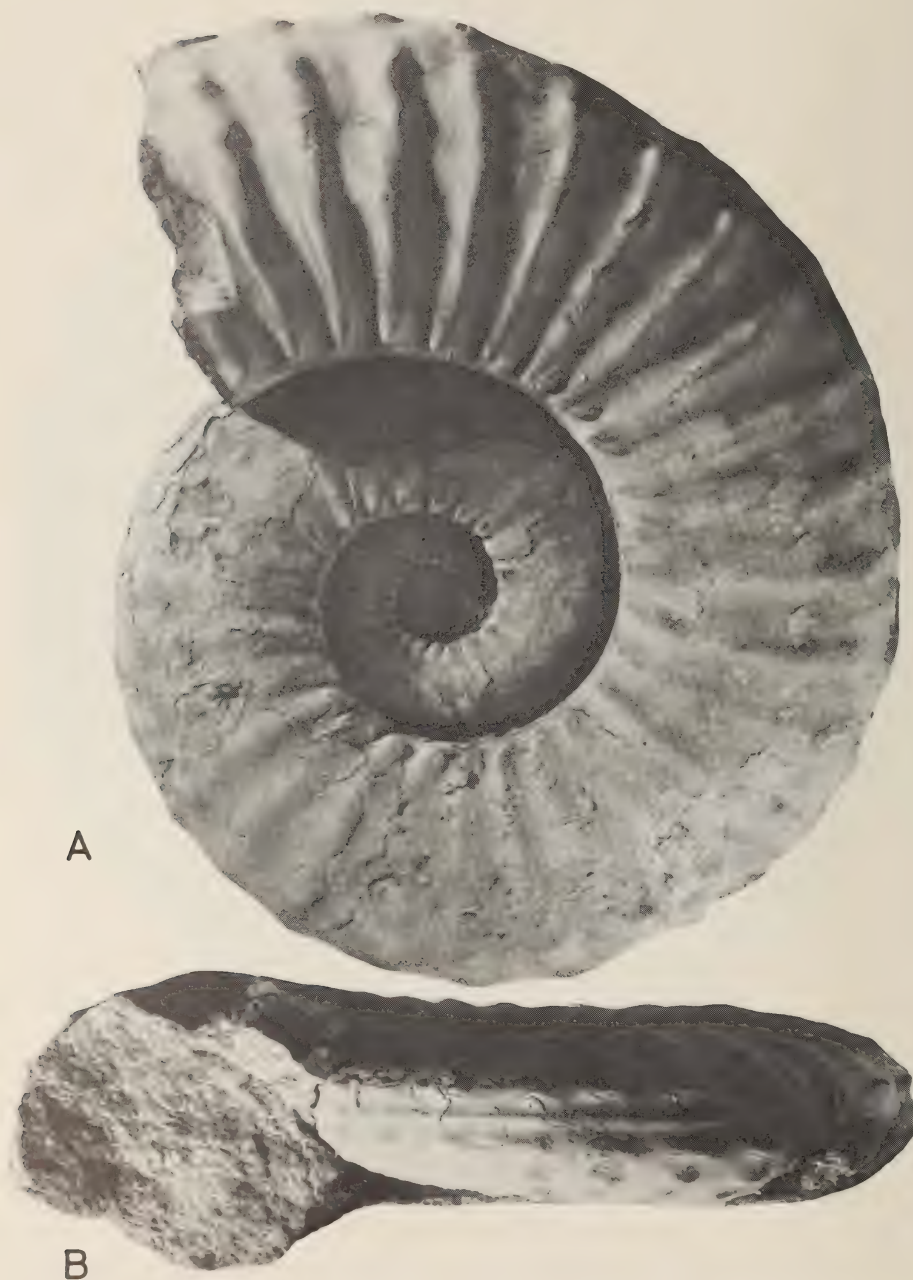


Fig. 188. *Submortoniceras woodsi natalense* ssp. nov. Holotype SAS-Z1875.  $\times 0,4$ .



Fig. 189. *Submortonicerias woodsi natalense* ssp. nov. Holotype SAS-Z1875. Close-up of inner whorls to show smooth flanks.





Fig. 190. *Submortoniceras woodsi natalense* ssp. nov. Paratype SAS-Z1138. Illustrating weak ornament on inner whorls.  $\times 1$ .

stronger submarginal (3) tubercles and visible, but much weaker than previously marginal (4) and external (5) tubercles.

These scant data, combined with our knowledge of the extreme intra-specific variation in *Submortoniceras chicoense*, as shown by Matsumoto (1959), or *Texanites soutoni* (Klinger & Kennedy herein p. 189), render interpretation of *Submortoniceras woodsi* impossible in terms of the holotype alone. Conse-



Fig. 191. *Submortonicerias woodsi natalense* ssp. nov. Paratype PCZ5884. Specimen with weak ornament on inner whorls.  $\times 0,57$ .

quently the authors interpret the species on the basis of topotype and more or less isochronous material.

As far as attenuation of ornament on the flanks is concerned, the holotype agrees well with the inner whorls of SAS-Z1875 (Fig. 188) or SAS-Z1138 (Fig. 187). The sutures, however, are completely different. The holotype has a suture with long and narrow lobes (Fig. 194A) as compared to the broad and

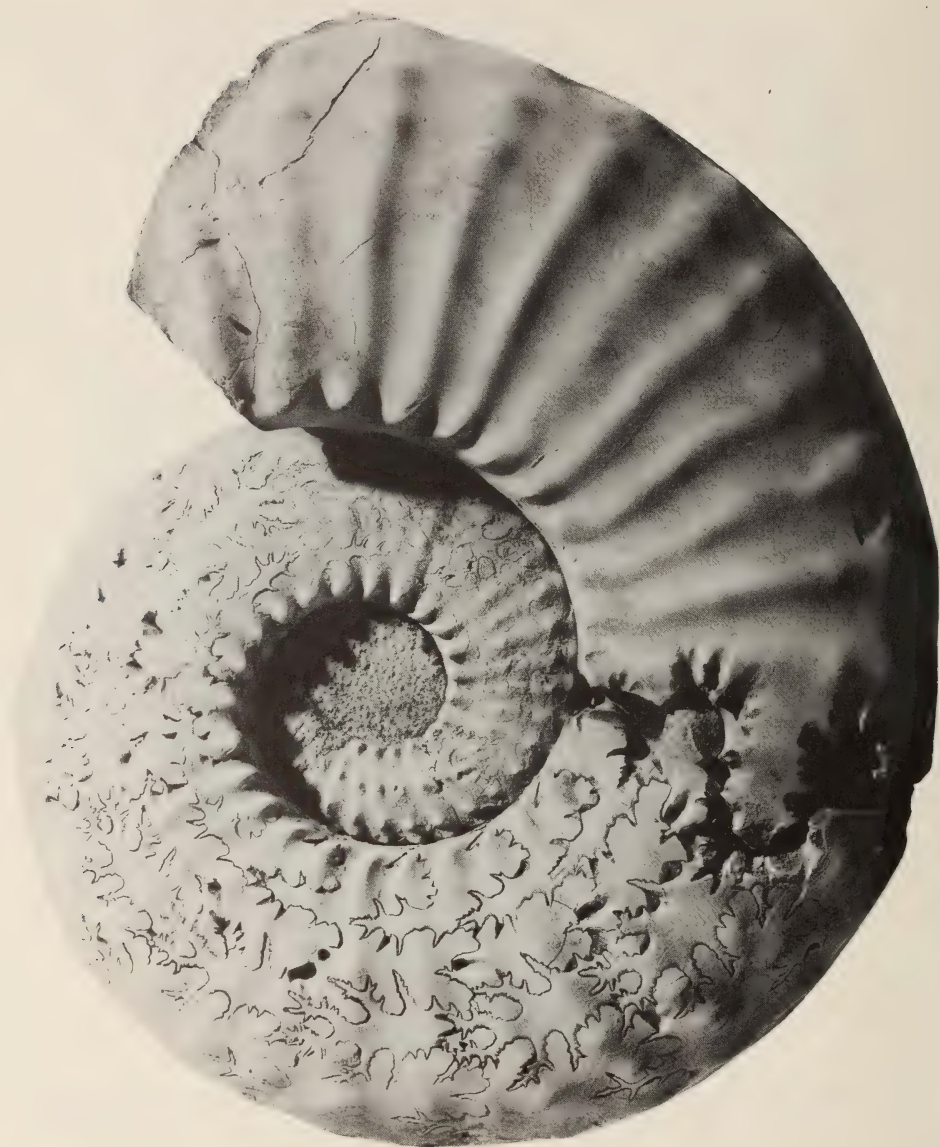


Fig. 192. *Submortonicerias woodsi woodsi* (Spath, 1921). SAM-PCZ5897. Specimen from Richards Bay with strong ornament on inner whorls.  $\times 0,65$ .





Fig. 193. *Submortonicerias woodsi woodsi* (Spath, 1921). SAM-PCP5716. Specimen from Umzamba with extremely strong ornament.  $\times 0,47$ .

short lobes of the latter two specimens (Fig. 195) and shows strong resemblance to *Texanites soutoni* s.s. in this respect. Topotype material from Umkwelane Hill figured by the authors (Kennedy & Klinger 1973, pl. 2 (fig. 3)) and a magnificent specimen from nearby at Richards Bay, SAM-PCZ5897 (Fig. 192), have similar long and narrow lobes, but distinct lateral ornament on the inner whorls. Thus, as in the case of *T. soutoni*, we are faced with two apparently different populations; one with smooth inner whorls and the other with variable ornament on the inner whorls. The specimens with smooth inner whorls generally have wide, short lobes and saddles whereas the specimens with

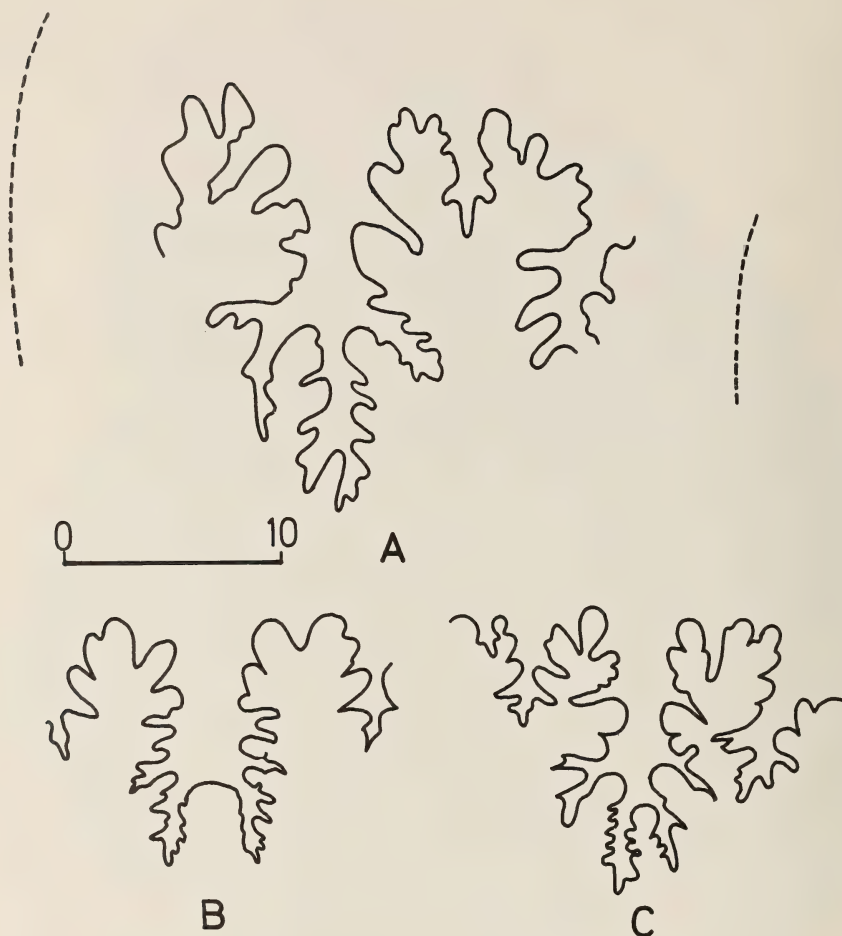


Fig. 194. *Submorticeras woodsi woodsi* (Spath, 1921). Suture lines. A. Holotype SAM-5451. B-C. SAM-PCZ5897.

coarsely ornamented inner whorls generally have long, thin lobes, but exceptions do occur. SAS-Z1893 (Fig. 196) has coarse ornament on the inner whorls but wide, open lobes. Comparable variation in suture line has been reported in *S. chicoense* by Matsumoto (1959: 129). Specimens with wide, open, blocky sutural elements appear predominantly in the False Bay region of Zululand, whereas the specimens with narrow, thin lobes and generally strong lateral ornament occur primarily in the southern regions of Umkwelane Hill, Richards Bay, Durban, and Pondoland.

Thus, in conformity with the procedure followed by the authors in *T. sou-toni* s.l. and *T. presoutoni* s.l., *S. woodsi* may be divided into two subspecies, *S. woodsi woodsi* (Spath) (holotype is SAM-5451, Fig. 186) and *S. woodsi*

*natalense* ssp. nov. (holotype is SAS-Z1875, Fig. 188), though bearing in mind that the dividing line here is extremely thin.

The holotype of *S. woodsi* was fitted into a dwarfed body chamber fragment from the Umkwelane Hill region. This chimera (Fig. 198) may possibly illustrate what the holotype of *S. woodsi woodsi* really looked like.

SAM-PCP5716 (Fig. 193) differs from the rest of the material in being tightest coiled, with an umbilical diameter of 32 per cent, thus approaching the limits of *S. condamyi* (described below), but still retaining a *T. soutoni*-like ornament of the body chamber.

Differences between *S. woodsi* s.l., and *S. condamyi* and *T. soutoni* are gradational, as outlined above (p. 177), and become indistinct in juvenile specimens. Difficulties arise especially in distinguishing between juveniles of *T. soutoni natalense* ssp. nov. with smooth whorls, e.g. SAS-Z1146 (Fig. 182), and the holotype of *S. woodsi*. The latter appears to be more narrowly umbilicate and has a more inflated whorl section. It thus appears as if acquisition of *Submortonicer* characteristics (in this case involution and compression of whorl section) takes place at varying and independent rates.

As the authors have pointed out previously (Kennedy & Klinger 1973: 103), *S. woodsi* may possibly be conspecific with a number of species described from Madagascar. In view of the poor definition of *S. woodsi* in terms of the holotype, and without being able to study the Madagascar specimens in their exact stratigraphic context, all comparisons must be viewed with utmost care.

*S. tenuicostulatum* has a slightly more compressed whorl section, but a comparable umbilical diameter (32–37%), and may possibly be a junior synonym of *S. woodsi*. Differences given by Collignon (1948: 97) pertaining to density of ribbing and spacing of the submarginal (3) and marginal (4) tubercles seem rather trivial, and, in fact, the specimen of *S. woodsi* figured by the authors from Durban (Kennedy & Klinger 1973, pl. 3 (fig. 2a–c)) (Fig. 199A–C) is

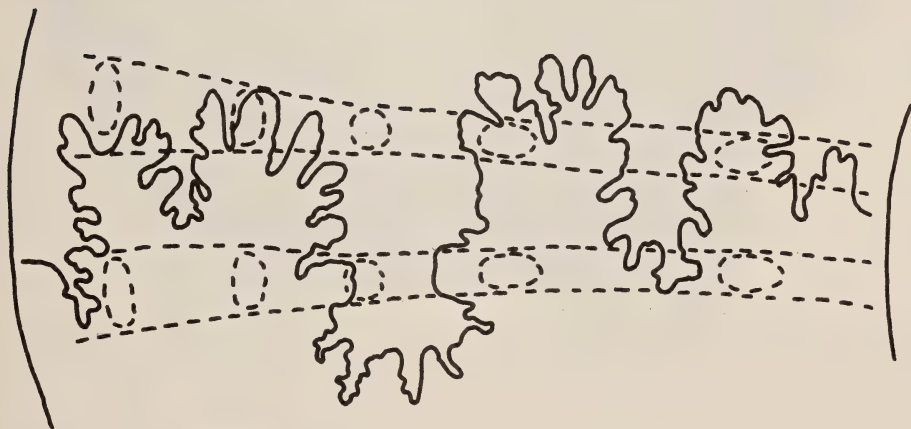


Fig. 195. *Submortonicer woodsi natalense* ssp. nov. SAS-Z1138. Suture line.  $\times 1$ .





Fig. 196. *Submortoniceras woodsi* s.l. SAS-Z1893. Specimen with broad lobes and saddles, but strong ornament on inner whorls.  $\times 0,55$ .



Fig. 197. *Submortoniceras woodsi natalense* ssp. nov. A. PCZ5854.  $\times 0,63$ . B, PCZ5897.  $\times 0,7$ .



Fig. 198. *Submortonicerias woodsi* s.l. (Spath, 1921). Chimera consisting of dwarfed outer whorl, partially septate, SAM-PCZ5896 from Umkwelane Hill, with the holotype, SAM-5451 fitted inside.  $\times 0,76$ .



remarkably similar to that of *S. tenuicostulatum* figured by Collignon (1948, pl. 19(13) (fig. 1-1b)). *S. tenuicostulatum*, however, appears to be of slightly younger age, occurring in the Middle Campanian Zone of *Pachydiscus grossouvrei* of Madagascar, compared to the Upper Santonian and/or Lower Campanian occurrence of *S. woodsi* in South Africa.

*S. collignoni* (= *Mortoniceras* (*Submortoniceras*) *woodsi* Collignon non Spath) may possibly be included in the synonymy of *S. woodsi*. The specimen figured by Collignon compares well with the inner whorls of *S. woodsi natalense*, as does the suture line figured by Collignon (1932: 36, text-fig. 19).

*S. punctatum* retains ornament to a larger diameter than *S. woodsi* and has an umbilical diameter transitional between that of *S. woodsi* and *S. condamyi*, and can probably be accommodated in either of these two species.

Of the *Submortoniceras* species described from Texas by Young (1963), *S. tequesquitense* seems very closely allied if not conspecific with *S. woodsi*. As far as relative proportions are concerned, dimensions of the two species overlap. *S. tequesquitense* has an umbilical diameter of 31 to 36 per cent, a reading of 41 per cent possibly being due to compression, and a Wb/Wh ratio of 0.93 to 0.69 decreasing with size, compared with an umbilical width of 32 to 39 per cent and a Wb/Wh ratio of 0.76 to 0.83 in *S. woodsi*. Young compared this species with *S. tenuicostulatum*, stating that it differed in having more prominent tuberculation and less bifurcations than *S. tenuicostulatum*. Apart from a slightly narrower whorl section, denser and more forwardly curved costation, there seems to be little difference between *S. tequesquitense* and *S. woodsi*. Another similarity between *S. tequesquitense* and *S. woodsi* is that Young (1963: 98) suggested that *S. tequesquitense* could be derived from *Texanites shiloensis* by caenogenesis, a situation comparable to that between *S. woodsi* and *T. soutoni*. Given more material, it may eventually prove possible to connect the sequence of *T. shiloensis*-*S. tequesquitense* to that of *T. soutoni* s.l.-*S. woodsi* s.l. at subspecific level as a North American equivalent.

The fragmentary specimen from the north-western side of False Bay described by Spath (1921: 308) as *Mortoniceras vanuxemi* probably also belongs to the group of *S. woodsi* rather than *S. vanuxemi*, of which no typical examples have as yet been found in Zululand. In view of the variation encountered in the sutures of *S. woodsi* s.l., Spath's (1921: 308) observation that the suture line of this specimen was similar to that of *S. woodsi* and *T. soutoni*, but differed on account of the terminations of the lateral lobe, poses no serious problem.

### Occurrence

Upper Santonian to Lower Campanian of Zululand and Pondoland, and rare in the Lower Campanian of Madagascar. Possible equivalents occur in the Lower Campanian of Texas.

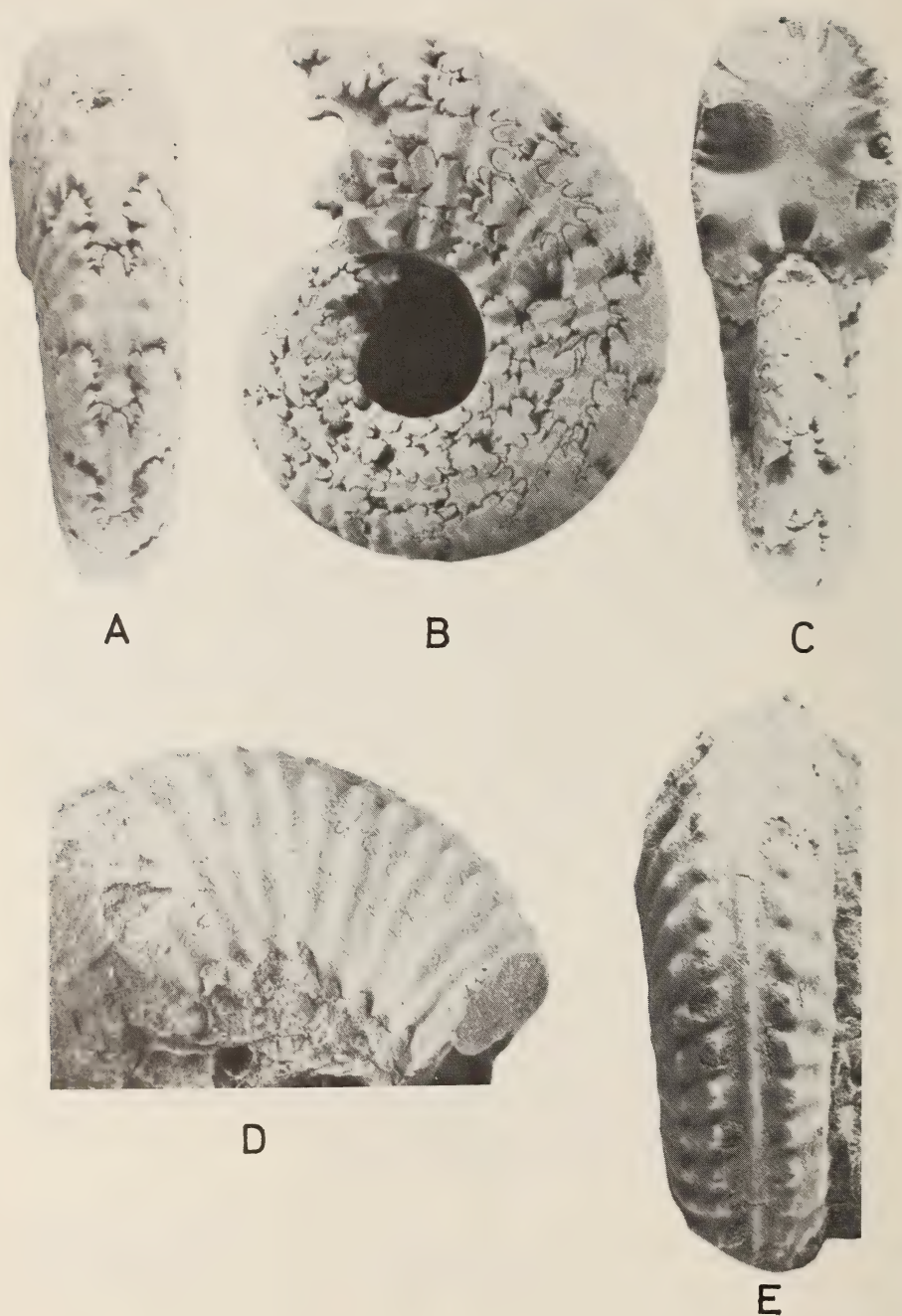


Fig. 199. *Submortonicerias woodsi woodsi* (Spath, 1921). A-C. UN6566. D-E. UN6566. (Specimens figured by the authors 1973, pl. 3 (fig. 2) and pl. 5 (fig. 3) from Durban.)  $\times 1$ .



Fig. 200. A. *Submortonicerases condamyi* s.l. (Collignon, 1948). SAS-Z1880.  $\times 0,7$ . B. *Submortonicerases woodsi* (Spath, 1921). (See Fig. 198.)  $\times 0,8$ .



*Submortonicerias condamyi* s.l. (Collignon, 1948)

Figs 200A, 201–209, 212–213

*Mortonicerias condamyi* Collignon, 1932: 36, pl. 5 (fig. 3–3b).*Mortonicerias* (*Submortonicerias*) *condamyi* (Collignon): Collignon, 1938: 76.*Submortonicerias condamyi* (Collignon): Collignon, 1948: 100, pl. 18(12) (fig. 2–2b), pl. 15.*Type*

Holotype is the specimen figured by Collignon (1932, pl. 5 (fig. 3–3b)) from the Lower Campanian of the environs of Berere, Madagascar.

*Material*

SAS–Z1140, Z1180, Z1952c, and SAM–PCZ5883, locality 105, south-eastern shores of False Bay, Zululand, St Lucia Formation, Upper Santonian to Lower Campanian; SAS–A2084, SAS–76/1, SAS–76, Z1756, SAM–PCZ5892–5894, all from locality 74, north-western shores of False Bay at Die Rooiwalle, St Lucia Formation, Upper Santonian to Lower Campanian; and SAM–PCP5717, Bed A7 locality 1, Umzamba Estuary, Pondoland, Umzamba Formation, Santonian/Campanian Boundary. SAM–PCP5885 and NMB–D1191 are from an unknown horizon at locality 1 at the Umzamba Estuary, Pondoland, Umzamba Formation, Santonian to Campanian.

*Dimensions*

|          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Ext.</i> |
|----------|----------|------------|------------|----------------|------------|-------------|-------------|
| Z1140    | 182,0    | 51,0(28,0) | 68,0(37,4) | 0,75           | 56,0(30,8) | 13 × 2      | 17 × 2      |
| SAS–76/1 | 199,0    | 56,0(28,1) | 83,0(41,7) | 0,67           | 65,0(32,7) | 25          | 42          |
| Z1952c   | 115,0    | 39,0(33,9) | 52,0(45,2) | 0,75           | 32,0(27,8) | 22          | 38          |
| A2084    | 195,0    | 57,0(29,2) | 75,0(38,5) | 0,76           | 67,0(34,4) | 24          | 37          |
| Z1180    | 215,0    | 54,0(25,1) | 78,0(36,3) | 0,69           | 70,0(32,6) | —           | —           |
| PCZ5893  | 147,0    | 47,0(31,9) | 63,0(42,9) | 0,74           | 46,0(31,3) | 28          | 40          |
| PCZ5892  | 141,0    | 47,0(33,3) | 56,0(39,7) | 0,84           | 53,0(37,6) | —           | —           |

*Description*

The material is very variable, but may be diagnosed as being narrowly umbilicate (*c.* 30%) with compressed whorl section and much attenuated ornament throughout.

Coiling in the earlier stages is tighter than in the adult stage, *c.* 23 per cent in SAS–Z1880 (Figs 201–202). SAM–PCZ5892 (Fig. 203) differs from the rest of the material in being much wider umbilicate, with an umbilical diameter of 37,6 per cent, coarser ornamented throughout, and it connects with *S. woodsi*.

The whorl section is higher than wide throughout, with weakly inflated flanks converging to a narrow venter (Figs 200A, 202B, 204A). Maximum whorl breadth is near midflank or towards the dorsal third of the flanks. The ratio of whorl breadth to whorl height is variable, as is the rounding of the venter (Figs 200A, 204A).

Ornament on the inner and outer whorls varies from coarsely ornamented to virtually smooth on the inner whorls, or attenuated to prominently penta-



Fig. 201. *Submortonicerias condamyi* (Collignon, 1948). SAS-Z1880.  $\times 0,64$ .

tuberculate on the body chamber, as the following specimens will illustrate. Specimens SAS-76/1 (Fig. 205), SAS-Z1880 (Fig. 201), SAS-Z1140, and SAS-A2084 have virtually smooth flanks on the inner whorls, save slight undulations indicative of incipient ribbing. In SAS-76/1 (Fig. 205), and SAS-Z1880 (Figs 201–202) parts of the earliest whorls are preserved, showing that the smooth stage is preceded by a more coarsely ornamented earlier stage. Slight swellings (?constrictions) are noticeable on the inner whorls of SAS-Z1880 (Fig. 202) and SAS-Z76/1 (Fig. 205). Specimens SAM-PCZ5893 (Fig. 206),



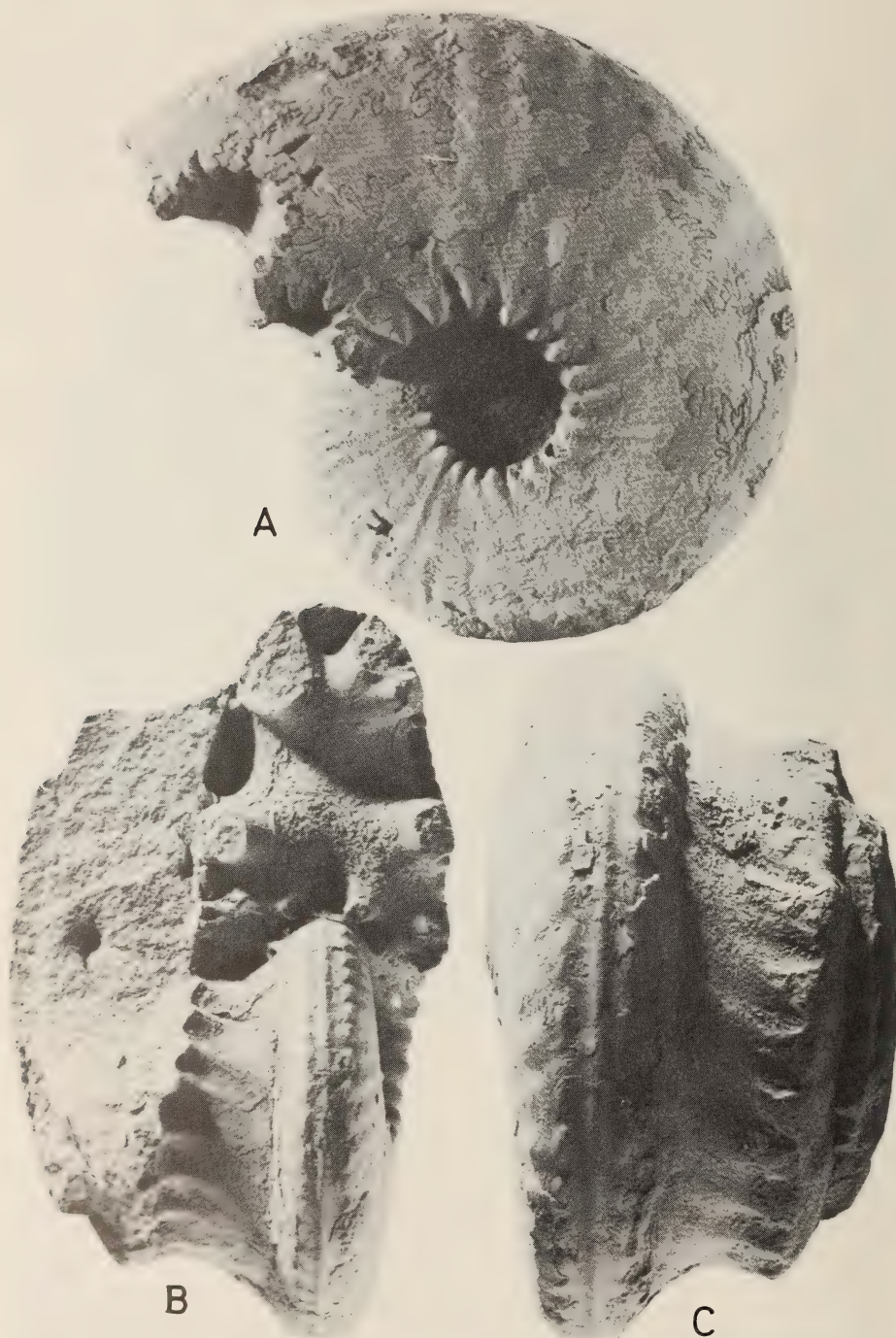


Fig. 202. *Submortonicerias condamyi* (Collignon, 1948). SAS-Z1880. Inner whorls.  $\times 1$ .  
(See also Fig. 201.)





Fig. 203. *Submortonicerias condamyi* (Collignon, 1948). SAM-PCZ5892. Atypical specimen, with wider umbilicus than normal and coarser ornament throughout, connecting with *S. woodsi*.  
× 1.

SAM-PCZ5894, and SAS-Z1952 have more prominent, though still weak, ornament on the inner whorls when compared with the preceding specimens. These specimens may be considered morphologically transitional to specimens with coarse ornament on the inner whorls, such as SAM-PCZ5717 (Fig. 207), SAS-Z1756 (Fig. 208) and SAM-PCZ5892 (Fig. 203).

All ornament, especially tuberculation, weakens progressively on the later part of the phragmocone at various stages, but toward, and on, the body

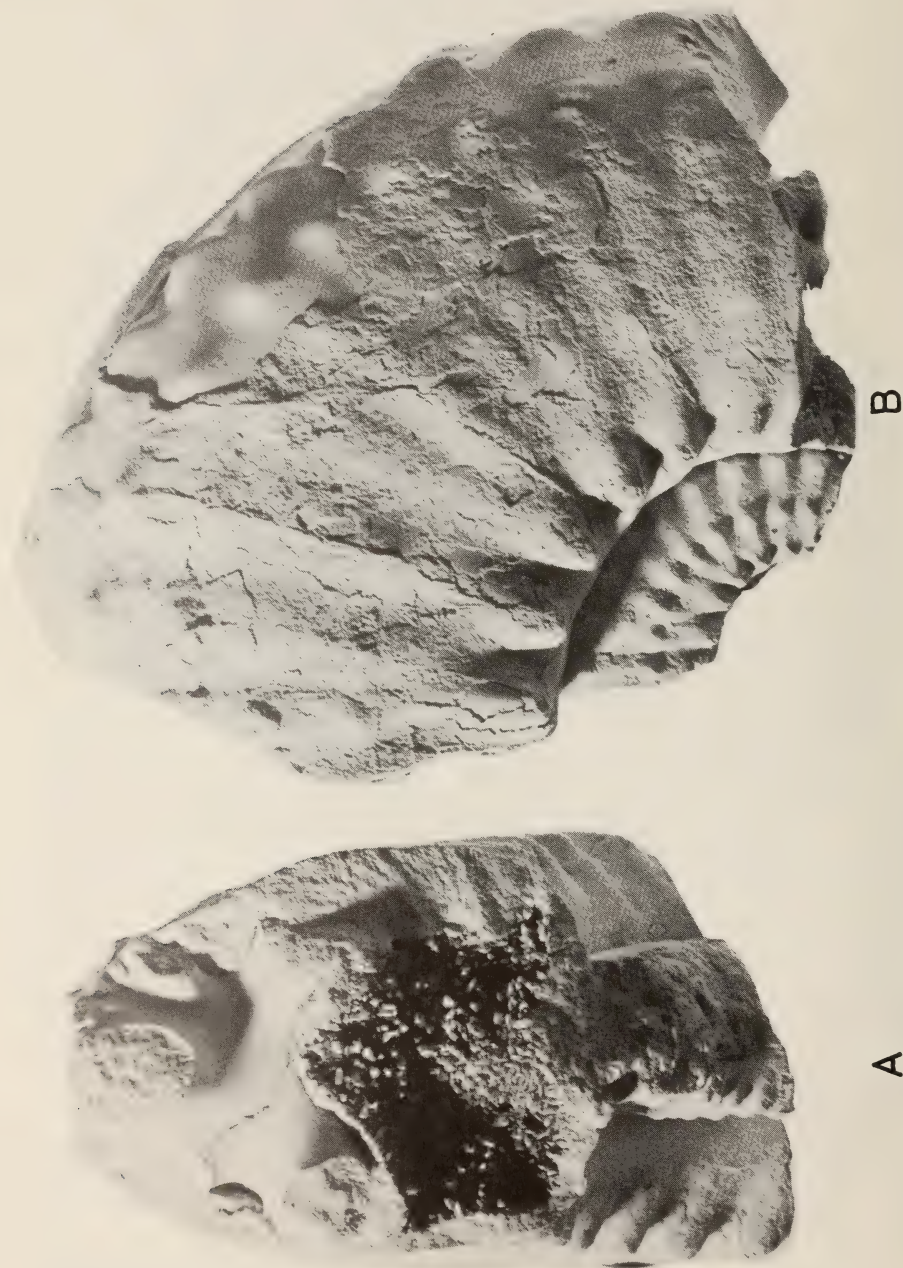


Fig. 204. *Submortoniceras condamyi* (Collignon, 1948). NMB-D1191.  $\times 1$ .



chamber, ribbing becomes more prominent again. In some specimens, e.g. SAS-Z1140 (Fig. 209) or SAS-A2084, distinct tuberculation develops on the body chamber, which acquires a distinct *Texanites*-like appearance. Spacing of ribbing on the body chamber, however, is variable. Specimens SAS-Z1756 (Fig. 208), SAS-76/1 (Fig. 205) and SAM-PCP5717 (Fig. 207) lack lateral tuberculation on the body chamber and may be regarded as being most *Submortonicer*as-like in this respect.

The venter is distinctly unicarinate throughout, except in SAS-Z1880 (Fig. 202) where the external (5) row of tubercles becomes elongated on the inner whorls at a diameter of c. 80 mm, thus creating the appearance of two lateral keels. On the body chamber of this specimen, however, the external (5) tubercles are distinctly separate, and the venter unicarinate.

The suture is variable, ranging from wide, blocky saddles and lobes as in SAS-Z1880 (Fig. 201), to long, narrow, thin-stemmed saddles and lobes as in SAM-PCP5717 (Fig. 207).

### Discussion

This species is here interpreted rather widely, but is characterized mainly by the narrow umbilicus.

Collignon (1948) described a number of *Submortonicer*as species from Berere, Madagascar, many of which appear comparable with, or identical to, the present material. Matsumoto (1959: 130) and Howarth (1966: 63) have already commented on the possible superfluity of some of the names applied to the Madagascar material, and these views are further enhanced by Matsumoto's description of the extremely variable Californian species *S. chicoense* as discussed above.

As shown in Figure 210, many of the Madagascar species occur together at the same restricted levels at Berere, whereas others have overlapping vertical ranges, all suggesting that systematics can be greatly simplified.

The South African material is comparable with the following Madagascar species, arranged in order of increasing umbilical width: *S. angusteumbilicatum*, *S. condamyi*, *S. spathi*, *S. renniei*, *S. punctatum*, *S. collignoni* and *S. tenuicostulatum*. Collignon (1948: 96 et seq.) separated his species mainly on the basis of details of whorl section, ornament and suture, but in view of the variation encountered in *S. chicoense* and *S. woodsi*, it is doubtful if these differences really warrant specific separation. Again, without having examined the material in its exact stratigraphic context, the authors are reluctant definitely to synonymize any of Collignon's species.

In terms of umbilical diameter, the South African material matches most closely with *S. condamyi*, although distinction between the various species in this respect is gradational (Fig. 211). Fortunately, Collignon (1932, 1948) provided ample illustrations of this species to illustrate the variation in ornament. His illustrations show that ornament varies from virtually smooth flanks (Collignon 1948, pl. 18(12) (fig. 2-2b)) through weakly and densely ornamented





Fig. 205. *Submortonicerias condamyi* (Collignon, 1948). SAS-76/1. Specimen with smooth inner whorls, but coarse ornament on body chamber.  $\times 0,65$ .

on the inner whorls (Collignon 1932, pl. 5 (fig. 3a-b)) to coarsely ornamented on the inner whorls (Collignon 1948, pl. 15). This variation in ornament compares favourably with that encountered in the South African material. In terms of ornament on the inner whorls, SAS-Z1756 (Fig. 208) and SAM-PCP5717 (Fig. 207) are comparable with Collignon's 1948, pl. 15 specimen; SAM-PCP5893 (Fig. 206) with the holotype; and SAS-Z1180 (Figs 201-202) with Collignon's 1948, pl. 18(12) (fig. 2-2b) specimen.



Fig. 206. *Submortonicerias condamyi* (Collignon, 1948). SAM-PCZ5893. Specimen with weak ornament on inner whorls.  $\times 0,85$ .

The suture lines of the Zululand specimens are similar to those of the large septate specimen figured by Collignon (1948, pl. 15) and of the holotype (Collignon 1932: 37, fig. 20), although the elements in the former are generally more 'blocky'. The Pondoland specimens, SAM-PCP5717 (Figs 207, 213A), SAM-PCP 5883 (Fig. 212) and NMB-D1191 (Figs 204, 213B), have more incised lobes and saddles and narrower elements. In accordance with the procedure followed above, the species may be divided into two subspecies on the basis of the suture line and more or less geographic restriction. The Zululand specimens with blocky elements are to be referred to *S. condamyi condamyi*, whereas the



Fig. 207. *Submortonicerias condamyi* (Collignon, 1948). Holotype of subsp. nov. *umzambiense*. SAM-PCP5717. Specimen with strong ornament on inner whorls.  $\times 0,62$ .

Pondoland specimens with narrower, more incised saddles and lobes are to be referred to *S. condamyi umzambiense* ssp. nov. (holotype is SAM-PCP5717 (Fig. 207) from Bed A7 locality 1, Umzamba Cliff, at the Santonian/Campanian boundary).

Development of tuberculation on the outer whorls, following the relatively smooth phragmocone stage in some of the Zululand specimens, e.g. SAS-



A2084, Z1140 (Fig. 209), is comparable with the trend displayed by *S. angustumbilicatum* Collignon; the whorl section in the latter species, however, seems to be more compressed, although the narrow, finely splayed lateral lobe (L) is comparable with *S. condamyi umzambiense* ssp. nov.

SAM-PCZ5893 (Fig. 206) has lateral ornament on the inner whorls very similar to that of *S. renniei* (cf. Collignon 1948, pl. 17 (fig. 1)), but lacks the very compressed whorl section ascribed to the species.



Fig. 208. *Submortonicerases condamyi* (Collignon, 1948). SAS-Z1756. Specimen with coarse ornament on inner whorls.  $\times 0.57$ .



Fig. 209. *Submortonicerias condamyi* (Collignon, 1948). SAS-Z1140. Specimen acquiring stronger *Texanites*-like ornament towards and on body chamber.  $\times 0,7$ .

| Species                         | Level at Berere |   |   |   |   |     |   |   |   |
|---------------------------------|-----------------|---|---|---|---|-----|---|---|---|
|                                 | 1               | 2 | 3 | 4 | 5 | 6   | 7 | 8 | 9 |
| <i>S. tenuicostulatum</i> . . . |                 | × | × |   |   | ×   |   |   |   |
| <i>S. dubium</i> . . . .        |                 | × |   |   | × | — × |   |   |   |
| <i>S. collignoni</i> . . . .    |                 |   |   | × | × |     | × | × |   |
| <i>S. punctatum</i> . . . .     |                 | × | × | × | × | — × |   |   |   |
| <i>S. condamyi</i> . . . .      |                 | × |   |   |   |     |   |   |   |
| <i>S. rarecostum</i> . . . .    |                 |   |   |   | × |     |   |   |   |
| <i>S. piveteaui</i> . . . .     |                 |   |   | × | × |     |   |   |   |
| <i>S. pauper</i> . . . .        |                 | × |   |   | × |     |   |   |   |
| <i>S. elimatum</i> . . . .      |                 | × |   |   |   |     |   |   |   |
| <i>S. angustumbilicatum</i> . . |                 |   |   |   | × |     |   |   |   |
| <i>S. spathi</i> . . . .        |                 |   |   |   | × | ×   | × |   |   |
| <i>S. rennei</i> . . . .        |                 | × |   |   |   |     |   |   |   |

Fig. 210. Table illustrating stratigraphic distribution of *Submortonicer* species at Berere, Madagascar.

SAS-Z1952c is similar to *S. punctatum* (cf. Collignon 1948, pl. 18(12) (fig. 1-1a) in becoming stronger ornamented towards the outer whorls, but does not have quite as strong ornament on the inner whorls.

*S. spathi* and *S. collignoni* have ornament comparable with this material, but much more compressed whorl sections.

Differences between *S. woodsi* s.l. as here interpreted, and *S. condamyi* s.l. are gradational. *S. condamyi* may be derived from *S. woodsi* s.l. through reduction of the umbilical diameter. Specimens SAM-PCZ5883 (Fig. 212) and SAS-A2084 may be regarded as being transitional between the two species in having a smaller umbilical diameter, but retaining to a certain extent the *Texanites*-like ornament.

Other *Submortonicer* species described from Madagascar by Collignon, e.g. *S. dubium*, *S. rarecostum*, *S. piveteaui*, *S. debile*, *S. pauper*, *S. elimatum*, and *S. rugetae*, all have much coarser ornament than the species allied or compared with *S. condamyi*. If differences in coarseness for forms  $\alpha$  and  $\gamma$  of *S. chicoense* (see Matsumoto 1959, pl. 32, pl. 34 (fig. 1)) are taken into consideration, however, one is again confronted with the possibility that we may be dealing with only one or a few very variable species.

Development of the pseudotricarinate venter at certain stages as in SAS-Z1880 (Fig. 202) is reminiscent of *S. mariscalense* Young from the upper part of the Lower Campanian of Texas. This latter species differs, however, in losing all ornament on the outer whorls, barring the bisulcate venter. Unfortu-



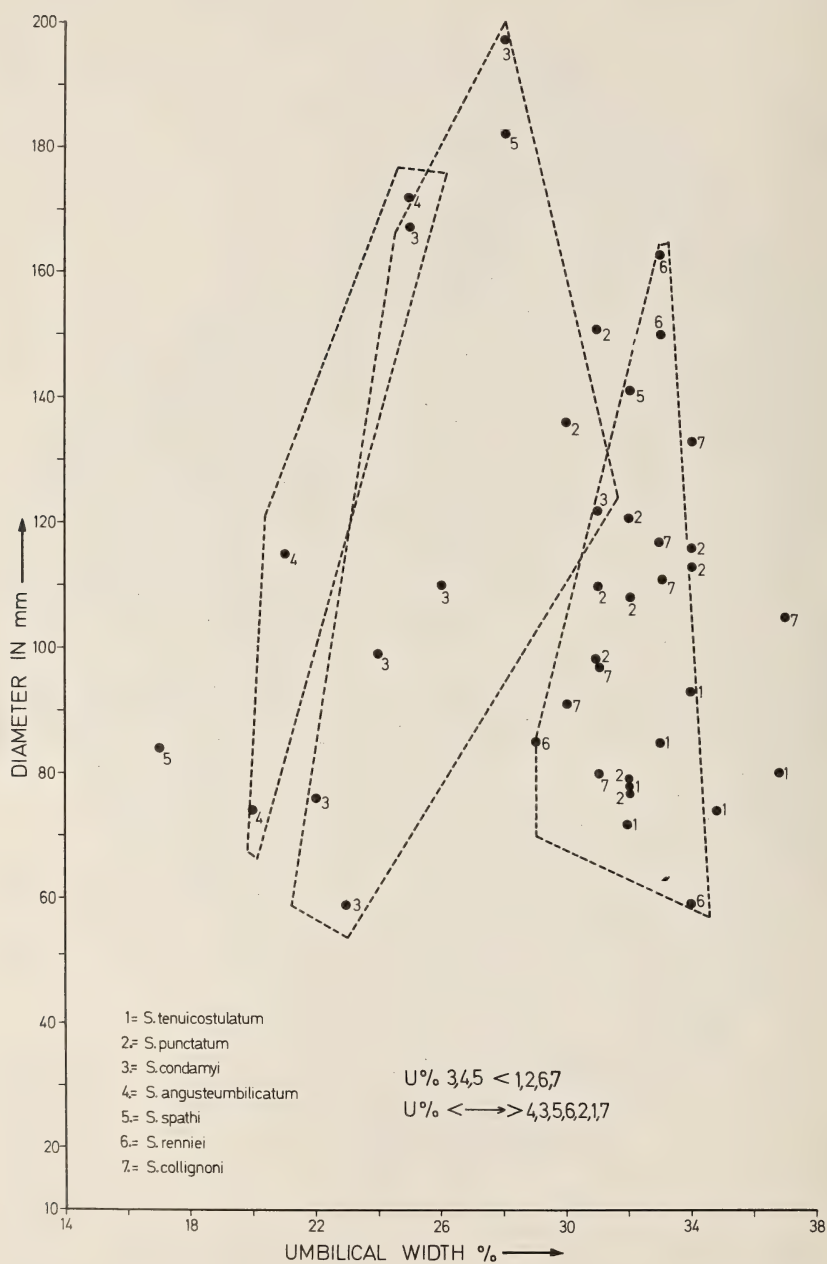


Fig. 211. Diagram to illustrate overlapping umbilical diameters of various *Submortonicerias* species.

nately, *S. mariscalense* is monotypic, thus precluding detailed comparison between the two species.

#### Occurrence

Upper Santonian to Lower Campanian of Pondoland and Zululand, and Lower Campanian of Madagascar.

#### Genus *Bevahites* Collignon, 1948

#### Type species

*Bevahites bevahensis* Collignon by original designation of Collignon (1948).

#### Diagnosis

Shell of variable size; generally small, with compressed or subsquare whorls.

The pentatuberculate stage is attained rapidly. Adult ornament is characterized by the proximity of the submarginal (3) and marginal (4) tubercles, and multiplication of the external (5) tubercles. Due to bifurcations many more external than internal rows of tubercle occur.

#### Discussion

*Bevahites* is poorly represented in the present collections which offer little basis for discussion of the genus. Originally *Parabevahites* was included in *Bevahites* as a subgenus, but most workers now follow Wright (1957: L432) in referring *Parabevahites* to *Paratexanites* as a subgenus, and even consider including *Parabevahites* in the synonymy of *Paratexanites* as is done here (see p. 14).

*Bevahites* is normally easy to distinguish from the other texanitid genera because of the proximity of the submarginal (3) and marginal (4) tubercles, and also because of the multiplication of the external row of tubercles. In this latter respect there is close comparison to *Menabites* s.s. Both have more external (5) tubercles than umbilical (1) ones, but those of *Bevahites* are also partially due to extensive bifurcations. It is difficult to distinguish between *Bevahites* species which lack the pronounced doubling of the submarginal (3) and marginal (4) tubercles, and species of *Menabites* s.s. which attain the pentatuberculate stage of development at an early stage.

From the list supplied below, it is clear that *Bevahites* is virtually restricted to Madagascar, with only two reports from the Gulf Coast of North America and specifically unidentifiable material from France (Fabre-Taxy 1963: 19–20). To this may now be added a new species and two doubtful contenders from the South African Cretaceous.

Species referred to *Bevahites* in the literature are:

*B. bevahensis* Collignon (1948: 84, pl. 11(5) (fig. 3–3b)) from the Upper Santonian of Madagascar and Gulf Coast of North America, possibly ranging up to the Lower Campanian (including Collignon's 'mutation' *intermedia*).

- B. dichotomus* Collignon (1948: 93, pl. 7(1) (fig. 4), pl. 17(11) (fig. 1-1b)) from the Lower Campanian of Madagascar.
- B. costatus* Collignon (1948: 90, pl. 7(1) (fig. 5), pl. 15(9) (fig. 1-1b)) from the Lower Campanian of Madagascar (including 'mutations' *crassicostata* Collignon, 1948: 91, pl. 15(9) (fig. 2-2b) from the Lower Campanian of Madagascar; *costulata* Collignon, 1948: 92, pl. 16(10) (fig. 2-2a) from the Middle Campanian of Madagascar; *rarecostata* Collignon, 1948: 92, pl. 16(10) (fig. 1) from the Middle Campanian of Madagascar; *inornata*



Fig. 212. *Submortonicerias condamyi* (Collignon, 1948). SAM-PCP5883.  $\times 0.8$ .



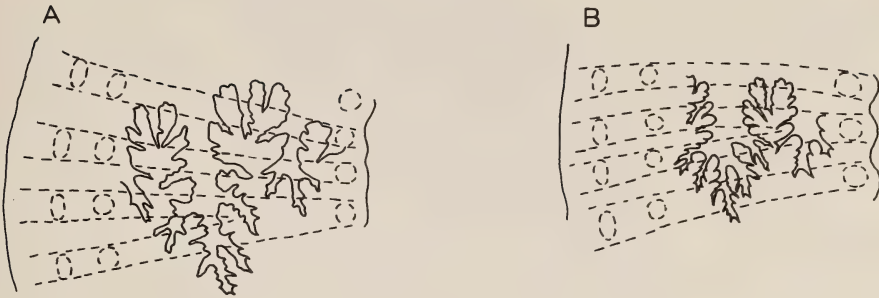


Fig. 213. *Submortonicer as condamyi* (Collignon, 1948). Suture lines of specimens referable to subspecies *umzambiense*. A. PCP5715. B. NMB-D1191.

Collignon, 1948: 93, pl. 16(10) (fig. 3–3b) from the Middle Campanian of Madagascar).

- B. costatus* Collignon *coahuilaensis* Young (1963: 96, pl. 47 (figs 1–4), pl. 71 (fig. 5), text-fig. 34b) from the Lower Campanian of the Gulf Coast of North America.
- B. curvicostatus* Collignon (1948: 87, pl. 13(7) (fig. 1–1b)) from the Lower Campanian of Madagascar.
- B. lapparenti* Collignon (1948: 88, pl. 14(8) (fig. 1–1b)) from the Middle Campanian of Madagascar.
- B. quadratus* Collignon (1948: 86, pl. 12(6) (fig. 3–3b)) from the Lower and Middle Campanian of Madagascar.
- B. romani* Collignon (1948: 95, pl. 17(11) (fig. 2–2a)) from the Middle Campanian of Madagascar.
- B. subbevahensis* Collignon (1948: 85, pl. 11(5) (fig. 4–4a)) from the Upper Santonian of Madagascar.
- B. subogivalis* Collignon (1948: 87, pl. 13(7) (fig. 2–2b)) from the Middle Campanian of Madagascar.
- B. subquadratus* Collignon (1948: 89, pl. 13(7) (fig. 3–3a, pl. 14(8) (fig. 2–2a)) from the Lower and Middle Campanian of Madagascar.

#### Occurrence

*Bevahites* occurs mainly in Madagascar, from the Upper Santonian to Middle Campanian and Upper Santonian of the North American Gulf Coast, and imprecise horizons in the Santonian and Campanian of Zululand. Specifically unidentifiable material was reported from the Lower Santonian of France (Fabre-Taxy 1963).

*Bevahites? enigma* sp. nov.

Fig. 214

*Holotype*

SAS-H68/2 (Fig. 214), locality 103, hill slopes near the Nyalazi River Estuary, Zululand, St Lucia Formation, Campanian I or II.

*Etymology*

Refers to uncertain generic allocation.

*Material*

The holotype only.

*Dimensions*

| <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb: Wh</i> | <i>U</i>   | <i>Ut</i> (1) | <i>Lt</i> (2) | <i>St</i> (3) | <i>Mt</i> (4) | <i>Et</i> (5) |
|----------|------------|------------|---------------|------------|---------------|---------------|---------------|---------------|---------------|
| 90,0     | 42,0(46,7) | 37,0(41,1) | 1,13          | 30,0(33,3) | 19            | ?             | 23            | 29            | 36            |

*Description*

The specimen is septate throughout, but lacks the very innermost whorls. The inner whorls preserved have a prominently depressed whorl section, much wider than high, but with increasing diameter the whorl section becomes more rounded, with a slightly outward-leaning umbilical wall, a prominent umbilical edge merging into little-inflated flanks which join imperceptibly with a broadly rounded to flattened venter.

At a diameter of 35 mm, ornament consists of a rounded umbilical (1) tubercle, a very prominent, radially elongated ventrolateral (submarginal) tubercle, closely situated indistinct marginal (4) tubercles and prominently rounded external (5) tubercles. The external (5), and in some cases already the submarginal (4), tubercles outnumber the submarginal (3) ones due to bifurcation or intercalation of ribbing near the venter at the site of the submarginal (3) tubercle. With increasing diameter, the submarginal (3) tubercles become weaker, and the distance between the latter and the marginal (4) tubercles becomes greater. Lateral (2) tubercles start appearing at a diameter of c. 45 mm on the dorsal quarter of the flanks as very indistinct little nodes.

With further increase in diameter, all tuberculation weakens and becomes subordinate to ribbing, and becomes equidistantly spaced over the flanks in the process.

The ratio of umbilical (1) to submarginal (3), marginal (4) and external (5) tubercles varies tremendously due to bifurcations and intercalations, as illustrated diagrammatically in Figure 214D. Bifurcations or intercalations may occur at the umbilical (1), the submarginal (3) or the marginal (4) tubercles, giving rise to the odd ratio of tubercles as provided in the list of dimensions. Thus, one umbilical (1) tubercle may correspond to up to four external (5) tubercles.

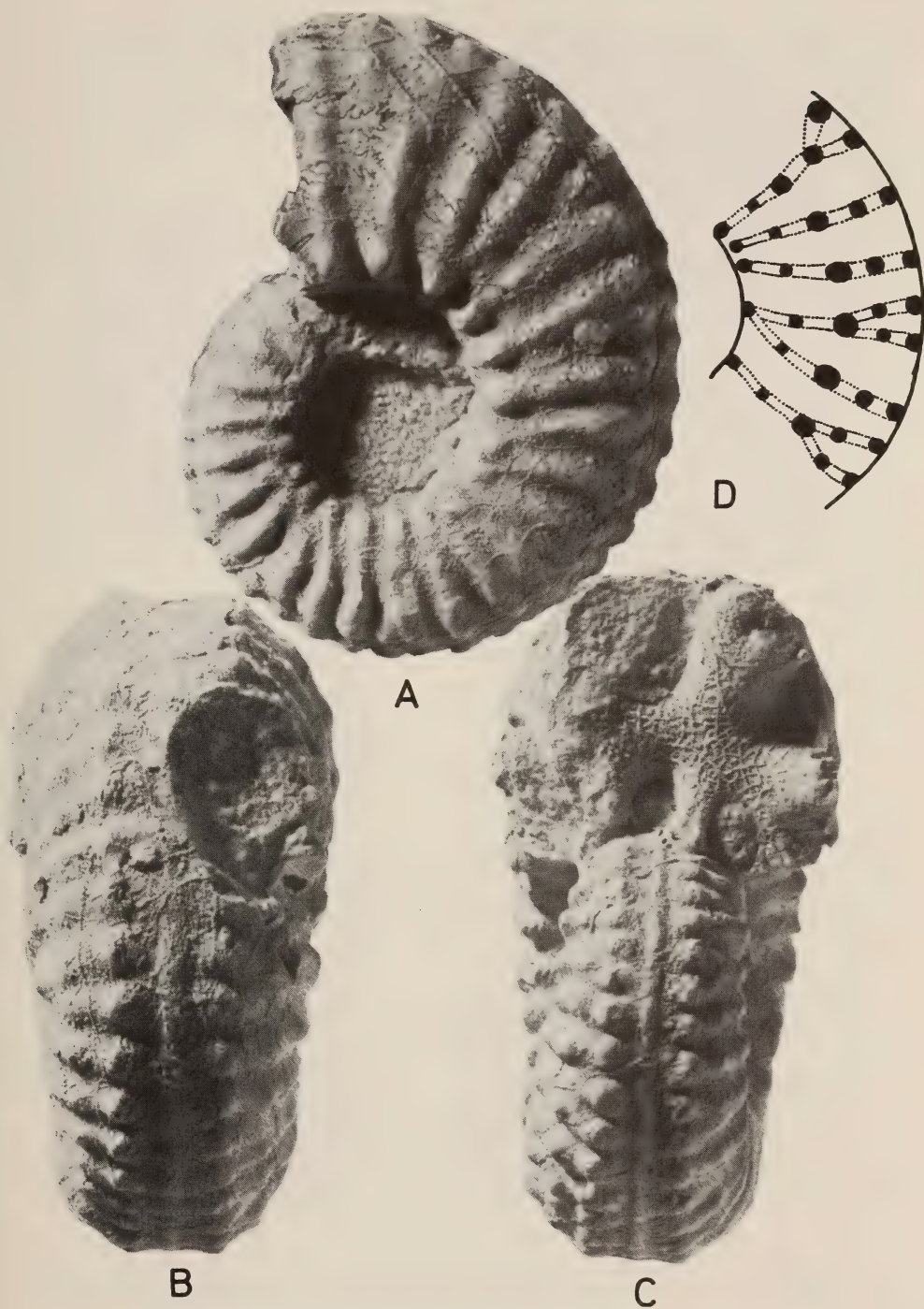


Fig. 214. *Bevahites? enigma* sp. nov. Holotype SAS-H68/2.  $\times 1$ .



The keel is entire and rather prominent on the early parts of the phragmocone, but tends to weaken on the last part preserved, and also shows slight undulations.

The suture is imperfectly preserved, showing a wide, bifid lateral lobe (L).

### Discussion

This species is readily recognized by the stout whorl section and by the irregularly bifurcating and intercalating ribbing, so much so that it requires specific rank, even though monotypic. The generic affinity of the species, however, is enigmatic, hence the name. The relative late persistence of a quadrituberculate stage places this species close to *Bevahites*, whereas the eventual equidistant pentatuberculate ornament is more in line with that of *Menabites*. For the present it is considered advisable to refer the species to *Bevahites* with a mark of interrogation, as it appears to fit best in the group of *Bevahites* sp. gr. ex. *quadratus* of Collignon (1948: 86) which includes the nominate species *B. quadratus*, *B. costatus*, *B. subogivalis*, and *B. lapparenti*. None of these species, however, has as narrow an umbilical width or as irregularly dichotomizing ornament. The closest ally amongst the former is probably *B. lapparenti*, which has a similar strongly developed ventrolateral tubercle in the early stages and which later splits into two.

As far as irregular bifurcations and intercalations are concerned, analogies are to be found in *B. bidichotomus*, but the latter has a much more compressed whorl section than the Zululand species.

*Bevahites* sp. A gr. ex. *B. subquadratus* Collignon, 1948

Fig. 215

### Material

NMB-D1185A and D1185B from an unknown locality in the Morrisvale area, probably the authors' (Kennedy & Klinger 1975) locality 147 of Santonian Age.

### Description

The two specimens differ considerably in terms of strength of ornament, but are both characterized by a compressed whorl section with maximum whorl breadth at the lateral tubercle.

NMB-D1185A (Fig. 215A) has smooth inner whorls up to a diameter of c. 15 mm. At a diameter of c. 30 mm virtually complete *Bevahites* ornament is present, though very weak, but the submarginal (3) tubercle appears absent at that stage. With increasing diameter, however, the ornament becomes stronger, especially the lateral (2) and external (5) tubercles.

NMB-D1185B (Fig. 215B-D), on the other hand, already has a distinct lateral ornament at 15 mm diameter, consisting of an umbilical (1) tubercle,

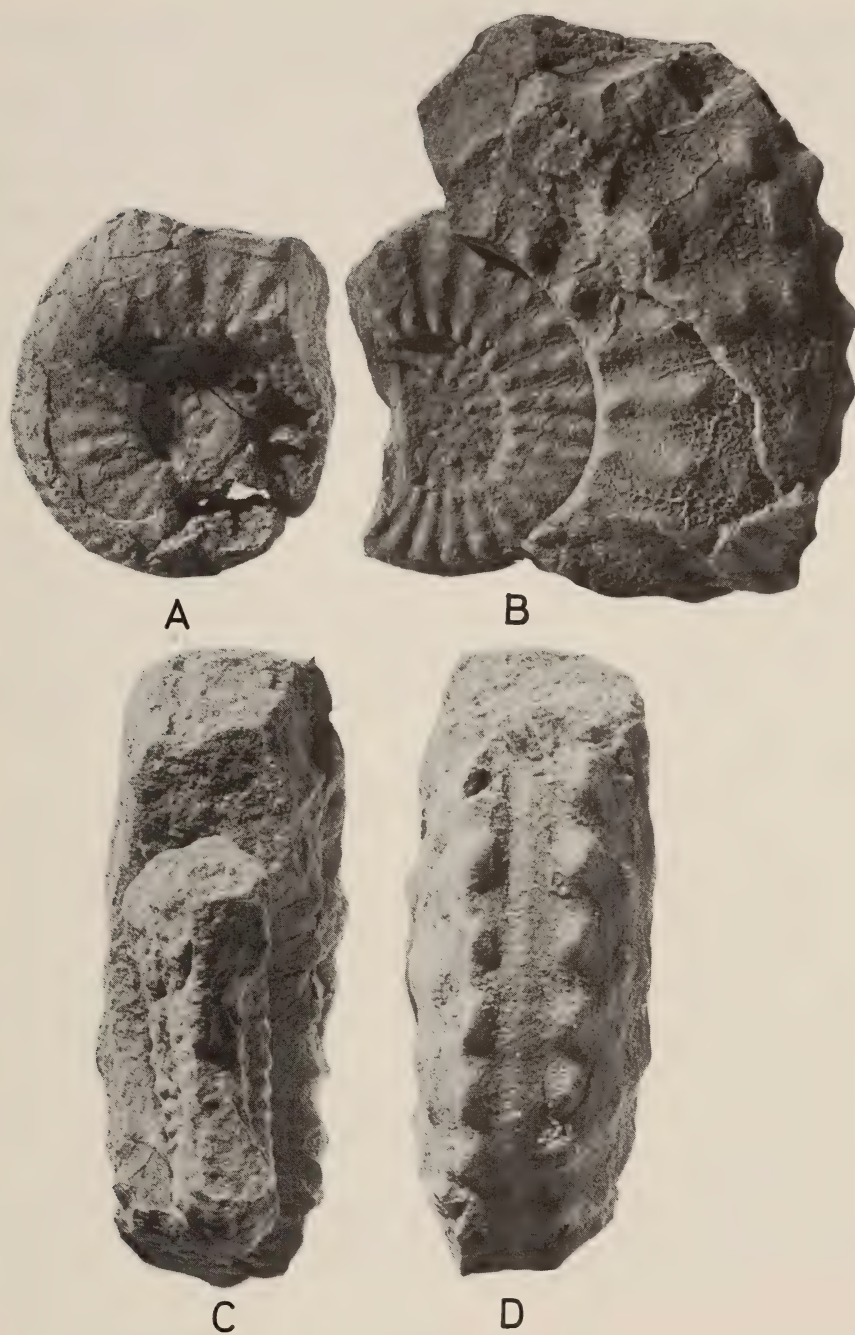


Fig. 215. *Bevahites* sp. A. gr. ex. *B. subquadratus* Collignon, 1948. A. NMB-D1185A.  
B-D. NMB-D1185B.  $\times 1$ .

connected by a stout rib to a prominent ventrolateral spine leaning against the umbilical wall. At 30 mm diameter the total ornament is visible, showing the typical joined submarginal (3) and marginal (4) tubercles and proliferation of the external (5) tubercles. The lateral (2) tubercle has apparently just appeared at this diameter, and is still weakly developed. Ornament strengthens with increasing diameter, and at a diameter of 50 mm the submarginal (3) and marginal (4) tubercles are completely separated. Ornament at this stage consists of radially elongated umbilical (1), very strong lateral (2), weak clavate submarginal (3) and marginal (4), and strong clavate external (5) tubercles.

Unfortunately the outer whorl of NMB-D1185B is crushed and eroded, but it shows the adult ornament consisting of strong umbilical, very strong lateral, and very weak marginal and submarginal and, again, strongly clavate external tubercles, and a very weak, narrow keel.

The suture is not exposed in either of the specimens.

### Discussion

Due to lack of precise stratigraphic data, it is not known if we are here dealing with one or two species, one with smooth inner whorls, and another with coarser-ornamented inner whorls, a situation perhaps comparable with that found in *Texanites soutoni* s.l. or *Plesiotechanites stangeri*. According to the data in the late E. C. N. van Hoepen's catalogue, the material was found near the confluence of the Msinduzi and Mkuze Rivers, which is probably the equivalent of, or close to, the authors' (Kennedy & Klinger 1975) locality 147 which was tentatively dated as Santonian.

For the above reasons it is considered best to refer to the material merely as *Bevahites* sp. A gr. ex. *B. subquadratus*, which includes the nominate species, *B. subquadratus*, *B. costatus* (including mutants *crassicosta*, *costulata*, *rarecosta* and *inornata*), *B. bidichotomus* and *B. romani*.

The inner whorls of *B. subquadratus* (see Collignon 1948, pl. 7(1) (fig. 5)) are similar to the coarsely ornamented inner whorls of NMB-D1185A (Fig. 215A), but ribbing is far more sinuous. Despite slight compression of the Zululand specimens, the holotype of *B. subquadratus* (Collignon 1948, pl. 14(8) (fig. 2-2a)) also appears more inflated.

*B. costatus*, including Collignon's (1948) 'mutations' *crassicostata*, *costulata*, *rarecosta* and *inornata* has a similar compressed whorl section, but in all cases lacks the strong development of external tubercles, and rather tends to have a more rounded venter.

*B. romani* is related to the Zululand material in the eventual separation of the submarginal tubercles, but differs mainly in strength of the different rows of tubercles and in the late development of the lateral tubercle.

### Occurrence

Probable Santonian of Zululand.



*Bevahites* sp. B. gr. ex. *B. subquadratus* Collignon, 1948

Fig. 216

### *Material*

NMB-D1067 from an unknown locality near the north-western end of False Bay, Zululand, probably at locality 74 towards the top of the section measured by Kennedy & Klinger (1975: 293, text-fig. 8).

### *Description and discussion*

The specimen consists of about a quarter of a whorl, is septate throughout and very sparsely ornamented. The whorl section is much higher than wide, with a vertical umbilical wall, slightly outward bulging flanks up to midflank, and then converging to a narrow, flat venter with a prominent row of clavate external (5) tubercles (Fig. 216B). Lateral ornament is very weak, consisting mainly of radially elongated umbilical (1) tubercles and about twice as many clavate external (5) tubercles. Lateral (2) tubercles merely appear as low nodes, and submarginal (3) and marginal (4) tubercles are absent for all practical purposes. The sutures are crowded, but appear to be very incised.

The whorl section is obviously that of the group of *B. subquadratus*, but on the basis of this limited material positive identification is not really possible. The whorl section is reminiscent of that of the *B. costatus* specimen figured by Collignon (1948, pl. 15(9) (fig. 2a)), but has a more flattened venter and better developed ventral tubercles.

This specimen differs from the previously described specimens of the group *B. subquadratus* in having a more compressed whorl section, and also in lacking the strong lateral ornament of the latter.

### *Occurrence*

Locality data are imprecise, but probably Santonian to Lower Campanian.

Genus *Menabites* Collignon, 1948

### *Type species*

*Menabites menabensis* Collignon, 1948, by original designation of Collignon, 1948.

### *Diagnosis*

*Menabites* is identified by the relatively long persistence of the trituberculate stage, sometimes apparently to maturity, and also by the multiplication of the tubercles of the external (5) row, numbering two to three times as many as the marginal (4) ones.

### *Discussion*

The whorl section, nature of ornamentation and persistence of the diagnostic trituberculate stage are very variable, so much so that, apart from

*Menabites* s.s., three other subgenera are recognized: *Bererella*, *Australiella* and *Delawareella*.

*Menabites* s.s. contains those forms in which the trituberculate stage passes relatively rapidly into a final pentatuberculate texanite stage.

*Bererella* (type species *M. (B.) bererensis* Collignon, 1948) contains widely umbilicate, flat forms with few and widely-spaced ribs.

*Australiella* (type species *M. (A.) australis* (Besairie)) contains those forms with wide whorl sections, sometimes strongly inflated and enormous lateral (2, 3, 4) tubercles, and may apparently retain this trituberculate stage to large diameters or throughout life.

*Delawareella* (type species *M. (D.) delawarensis* Collignon) contains forms with numerous ribs, closely spaced, often flexuous, and with attenuated ornament and a narrow umbilicus.

Of all the described species and subspecies of *Menabites* s.l., about half appear to be restricted to Madagascar; the remaining known reports are from the Gulf Coast and adjacent areas of North America, Zululand and Hokkaido. As in *Submorticeras*, it is difficult to decide whether this distribution pattern reflects real geographically separated species groups in each area, or, rather, the individual systematicist's approach towards classification.

*Menabites* s.l. is very easy to distinguish from the majority of other texanites on account of the multiplication of the external row of tubercles, but also on stratigraphic grounds, being apparently the last texanites to survive of a very successful lineage dating from the Upper Coniacian.

Differentiation between the four subgenera as outlined above sometimes becomes difficult, as characteristics often overlap, and the diagnostic differences appear to be based on ontogenetic features.

Further differences arise in distinguishing between *Menabites* s.s. and *Bevahites*, both of which have a multiplied external row of tubercles.

The basic distinguishing feature between *Menabites* s.s. and *Bevahites* is the longer persistence of the trituberculate stage in the former, and, to a lesser extent the proximity of the submarginal (3) and marginal (4) tubercles in *Bevahites*, although application of this criterion sometimes becomes subjective as the Zululand material shows.

Unless the inner whorls are preserved to reveal details of ontogeny, it is difficult to distinguish between late representatives of *Submorticeras*, e.g. *S. johannisludovici* Collignon, and smooth forms of *Menabites* (*Delawareella*).

The Zululand specimens of *Menabites* are very large, with diameters of up to 700 mm in one *M. (Delawareella)* species. This, combined with the general lack of the early inner whorls, makes it difficult to identify these specimens with the much smaller species described from Madagascar. Difficulties occur especially in the interpretation of *M. (Australiella)* species. Apart from the fact that all the Zululand representatives of this subgenus are highly variable, they grow to much larger diameters, and in doing so pass from the typically trituberculate *Australiella* stage to a pentatuberculate *Menabites* or *Bererella* stage. Unfortu-

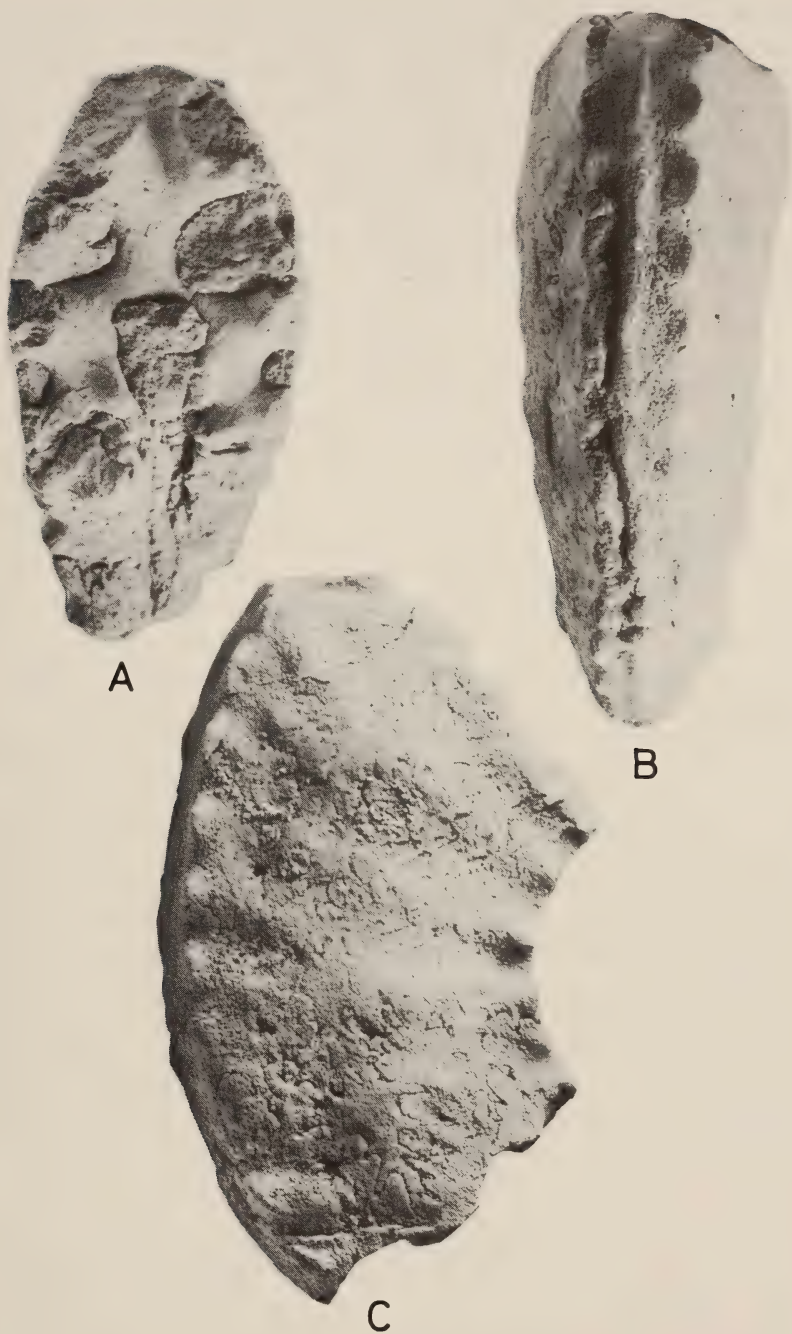


Fig. 216. *Bevahites* sp. B. gr. ex. *B. subquadratus* Collignon, 1948. NMB-D1067.  $\times 1$ .



nately, the authors have insufficient data on the Madagascan material to find out whether these *Australiella* species were, in fact, all adult or immature.

Phylogenetic relationships between *Menabites* s.l. and the other texanite genera, and even between the subgenera within *Menabites*, are not quite clear.

In Madagascar, *Menabites* s.s. starts appearing in the upper part of the Lower Campanian, Zone of *Menabites boulei* and *Anapachydiscus arrialoorensis*, but is replaced by representatives of *Australiella*, *Delawareella* and *Bererella* in the Middle Campanian. Data on the first appearance of *Menabites* in Zululand are scant, but the abundant occurrence of *Australiella* and *Delawareella* at the south-western tip of the Nibela Peninsula seems to suggest the same temporal sequence.

This, however, is at variance with the views held by Matsumoto (1970: 298) and Young (1963: 107). Their views are supported by the alleged occurrence of *Australiella* in sediments of Santonian age. Locality data on *Australiella austiniensis* Young are confusing (Young 1963: 116), and Young considered it to be 'probably Lower Santonian, but could be lowest Campanian'(!). *Australiella* sp. aff. *A. pattoni* in Matsumoto (1970: 300) also lacks a firm dating and was dated as 'probably Santonian' (Matsumoto 1970: 300).

On the basis of the Malagasy and Zululand material, the authors would rather be inclined to derive *Australiella*, *Delawareella* and *Bererella* from *Menabites* s.s.

The origin of *Menabites* s.l. is obscure, and the Zululand material provides no direct information. Young (1963: 107) and Matsumoto (1970: 289) are inclined to derive *Menabites* (or *Australiella*) from *Protexanites*. *Protexanites* (*Pleurotexanites*) from the Mid-Santonian of Madagascar only has three rows of tubercles, of which the external ones are multiplied as in *Menabites* s.l., and is thus a possible ancestral form.

Another possibility, which closes the time gap between Mid-Santonian and Early Campanian, is *Bevahites*. Through reduction of the lateral tubercle and strengthening of the double ventrolateral tubercle, the initial trituberculate situation as in early *Menabites* s.s. ontogeny can be derived.

Clearly, no satisfactory answer to this question will be found unless based on detailed collecting.

Venzo's (1936: 88, pl. 3 (fig. 12)) *Mortonicerias vinassai* is definitely not a *Menabites*, but probably a *Forresteria*. The locality, 'Riva sinistra del basso Umsinene' corresponds to the authors' (Kennedy & Klinger 1975) locality 72 or 73 of Upper Coniacian or Lower Santonian age.

Species referred in literature to subgenus *Menabites* are:

- M. (Menabites) belli* Young (1963: 106, pl. 54 (fig. 1), pl. 58 (fig. 2), pl. 70 (figs 2-4, 7), text-fig. 15a) from the Lower Campanian of the Gulf Coast of North America.
- M. (Menabites) boulei* Collignon (1948: 14, pl. 22 (fig. 1-1b)) from the Lower and Middle Campanian of Madagascar.

- M. (Menabites) breistrofferi* Collignon (1948: 19, pl. 24 (fig. 1-1b)) from the Campanian of Madagascar.
- M. (Menabites) cottreoui* Collignon (1948: 16, pl. 23 (fig. 2-2b)) from the Middle Campanian of Madagascar.
- M. (Menabites) dabolavaensis* Collignon (1948: 20, pl. 24 (fig. 3-3a)) from the Lower and ?Middle Campanian of Madagascar.
- M. (Menabites) densinodosus* (Renz) (1936: 8, pl. 2 (fig. 1-1a)) from the Lower Campanian of the Gulf Coast of North America.
- M. (Menabites) gignouxii* Collignon (1948: 15, pl. 22 (fig. 2-2b)) from the Campanian of Madagascar.
- M. (Menabites) internodosus* (Renz) (1936: 10, pl. 3 (fig. 2-2b)) from the Lower Campanian of the Gulf Coast of North America.
- M. (Menabites) jacobi* Collignon (1948: 13, pl. 20 (fig. 3-3b)) from the Middle Campanian of Madagascar.
- M. (Menabites) lenoblei* Collignon (1948: 19, pl. 24 (fig. 1-1b)) from the Campanian of Madagascar.
- M. (Menabites) latissimus* Collignon (1969: 192, pl. 594 (fig. 2244)) from the Lower Campanian of Madagascar.
- M. (Menabites) mazenoti* Collignon (1948: 11, pl. 20 (fig. 2-2a)) from the Middle Campanian of Madagascar.
- M. (Menabites) menabensis* Collignon (1948: 7, pl. 17 (figs 3a-b, 4-4a), pl. 18 (fig. 1-1b)) from the Lower Campanian of Madagascar.
- M. (Menabites) menabensis* var. *lata* Collignon (1948: 9, pl. 18 (fig. 2-2b)) from the Lower Campanian of Madagascar.
- M. (Menabites) multiformis* Collignon (1948: 12, pl. 7 (fig. 8-8b), pl. 19 (fig. 1-1a)) from the Middle Campanian of Madagascar.
- M. (Menabites) paucituberculatus* Collignon (1948: 21, pl. 24 (fig. 2-2a)) from the Middle Campanian of Madagascar.
- M. (Menabites) rarecostus* Collignon (1969: 194, pl. 595 (fig. 2246)) from the Lower Campanian of Madagascar.
- M. (Menabites) savornini* Collignon (1948: 9, pl. 7(1) (fig. 9-9a), pl. 19 (figs 2-2a, 3-3a), pl. 20 (fig. 1), pl. 21 (figs 1-1b, 2-2b)) from the Middle Campanian of Madagascar.
- M. (Menabites) tsirananaei* Collignon (1969: 196, pl. 595 (fig. 2247)) from the Lower Campanian of Madagascar.
- Menabites* s.l. *walnutensis* Young (1963: 109, pl. 58 (figs 1, 4), text-figs 20ef, 26k) from a loose block, presumably Lower Campanian of the Gulf Coast region of North America.

Species referred to subgenus *M. (Delawarella)* in the literature are:

- M. (Delawarella) bassae* Collignon, 1948 (Basse 1931: 41, pl. 6 (figs 1-4); see also Collignon 1948: 36, pl. 31 (fig. 3)) from the Middle Campanian of Madagascar.

- M. (Delawareella) campaniensis* (De Grossouvre) (1894: 84, pl. 13 (figs 1a–b, 3a–b)) from the Middle Campanian of France, and from the Lower Campanian of the Gulf Coast of North America.
- M. (Delawareella) danei* Young (1963: 114, pl. 57 (fig. 6), pl. 62 (figs 1–2), pl. 64 (figs 1, 5), pl. 65 (figs 1–2), pl. 66 (figs 3–4), text-figs 24c, 33b) from the Lower Campanian of the Gulf Coast of North America.
- M. (Delawareella) delawarensis* (Morton) (1830: 244, pl. 2 (fig. 4)) from the Middle Campanian of Delaware, New Jersey and Texas.
- M. (Delawareella) jeanneti* Collignon (1948: 34, pl. 30 (fig. 3–3b), pl. 31 (fig. 1–1b)) from the Middle Campanian of Madagascar.
- M. (Delawareella) jeanneti* var. *compressa* Collignon (1948: 36, pl. 31 (fig. 2–2a)) from the Middle Campanian of Madagascar.
- M. (Delawareella) roedereri* Collignon (1948: 38, pl. 32 (fig. 1–1b)) from the Middle Campanian of Madagascar.
- M. (Delawareella) sabinalensis* Young (1963: 112, pl. 54 (fig. 2), pl. 63 (figs 1, 3–4), text-figs 20c, 21e, 26c) from the Lower Campanian of the Gulf Coast of North America.
- M. (Delawareella) subdelawarensis* Collignon (1948: 32, pl. 29 (figs 1a–b, 2a–b)) from the Middle Campanian of Madagascar.
- M. (Delawareella) subdelawarensis* var. *lenticularis* Collignon (1948: 43, pl. 30 (fig. 1–1a)) from the Middle Campanian of Madagascar.

The following species have been referred to subgenus (or genus) *Australiella* in the literature:

- M. (Australiella) australis* (Besairie) (1930: 638, pl. 64 (fig. 2–2a)) from the Middle Campanian of Madagascar.
- M. (Australiella) australis ingens* Collignon (1970: 62, pl. 633 (fig. 2334)) from the Middle Campanian of Madagascar.
- M. (Australiella) antsirasiraensis* Collignon (1948: 28, pl. 28 (fig. 3–3a)) from the Middle Campanian of Madagascar.
- M. (Australiella) austinensis* Young (1963: 115, pl. 64 (figs 3–4), pl. 65 (fig. 6), pl. 67 (figs 4–6), text-fig. 28e) from an imprecise horizon in the Gulf Coast, reported as Senonian and ‘probably Lower Santonian, but could be lowest Campanian’ (Young 1963: 116).
- M. (Australiella) besairiei* (Collignon) (1938: 75, pl. 4 (fig. 2–2b)) from the Middle Campanian of Madagascar.
- M. (Australiella) coronata* Collignon (1970: 56, pl. 631 (fig. 2328)) from the Middle Campanian of Madagascar.
- M. (Australiella) moreti* Collignon (1948: 28, pl. 28 (fig. 2–2b)) from the Middle Campanian of Madagascar.
- M. (Australiella) pattoni* Young (1963: 116, pl. 65 (figs 4–5), pl. 66 (figs 1–2, 5–6), pl. 68 (figs 1–3, 6), text-figs 24b, 26h, 33ac, 34dg) from the Lower Campanian of the Gulf Coast of North America, and, doubtfully, from an unknown horizon, possibly Santonian, of Japan.



- M. (Australiella) souqueti* Collignon (1970: 59, pl. 623 (fig. 2332)) from the Middle Campanian of Madagascar.
- M. (Australiella) subaustralis* Collignon (1948: 27, pl. 27 (fig. 3-3a)) from the Middle Campanian of Madagascar.
- M. (Australiella) tintanti* Collignon (1970: 57, pl. 631 (fig. 2330)) from the Middle Campanian of Madagascar.
- M. (Australiella) welderi* Young (1963: 117, pl. 65 (fig. 3), pl. 68 (figs 4-5, text-fig. 25kn) from the Lower Campanian of the Gulf Coast of North America. Species referred to subgenus *Bererella* in literature are:
- M. (Bererella) aculeata* Collignon (1948: 23, pl. 26 (fig. 2-2a)) from the Middle Campanian of Madagascar.
- M. (Bererella) atropsi* Collignon (1969: 200, pl. 598 (fig. 2250)) from the Lower Campanian of Madagascar.
- M. (Bererella) bererensis* Collignon (1948: 22, pl. 25 (fig. 1-1b)) from the Lower Campanian of Madagascar.
- M. (Bererella) bererensis* mut. *multicostata* Collignon (1948: 198, pl. 27 (fig. 1-1b)) from the Lower Campanian of Madagascar.
- M. (Bererella) bererensis compressa* Collignon (1969: 200, pl. 598 (fig. 2251)) from the Lower Campanian of Madagascar.
- M. (Bererella) bifidata* Collignon (1948: 25, pl. 26 (fig. 3)) from the Middle Campanian of Madagascar.
- M. (Bererella) rochi* Collignon (1948: 25, pl. 27 (fig. 2-2b)) from the Middle Campanian of Madagascar.
- M. (Bererella) tenuis* Collignon (1948: 24, pl. 25 (fig. 2-2b)) from the Middle Campanian of Madagascar.

### Occurrence

*Menabites* s.l. occurs profusely in the Lower and Middle Campanian of Madagascar and Zululand, and in reduced numbers in the Gulf Coast and adjacent regions of North America and also Hokkaido, where they allegedly occur as early as Santonian. A single species is known from the Campanian of France.

### *Menabites (Menabites) boulei* Collignon, 1948

Fig. 217

*Menabites boulei* Collignon, 1948: pl. 22 (fig. 1-1b); 1969: 192, pl. 594 (fig. 2243).

### Type

Holotype is the specimen figured by Collignon (1948, pl. 22 (fig. 1-1b)) by original designation.

### Material

SAM-PCZ5690, locality 100, north of Nkundusi, Zululand, St Lucia Formation; originally considered to be Lower Santonian, but, on the basis of this identification, now dated as Lower Campanian.



Fig. 217. *Menabites (Menabites) boulei* Collignon, 1948.  
SAM-PCZ5690.  $\times 1$ .

#### *Dimensions*

| <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i>   | <i>Ext.</i>   |
|----------|------------|------------|----------------|------------|---------------|---------------|
| 101,0    | 33,0(32,6) | 39,0(38,6) | 0,85           | 36,0(35,6) | 11 $\times$ 2 | 18 $\times$ 2 |

#### *Description*

Unfortunately the innermost whorls are lacking, but parts of them and their impressions indicate the presence of a large, ventrolateral *Menabites* node, confirming the generic allocation.

The umbilical width is 35 per cent of the total diameter, and the dorsal zone of impression very shallow, with whorl overlap scarcely to the marginal (4) tubercle. The whorl section is basically compressed, higher than wide, with slightly inflated flanks converging to a flattened venter.

Ornament in the species is very strong, consisting of conical, equally strong umbilical (1) and lateral (2) tubercles, very strong conical to radially elongated

submarginal (3) tubercles, and very weak clavate marginal (4) and stronger clavate external (5) tubercles.

Bifurcations or intercalations occur at the submarginal (3) tubercle, but not regularly, as single ribs occur as well, resulting in a ratio of umbilical to external tubercles of slightly less than 1 : 2.

The suture is poorly exposed, but features a large lateral lobe (L).

### Discussion

This species is easily characterized by the strength of the ornament on the outer whorl.

*M. (M.) boulei* and *M. (M.) menabensis* have similar inner whorls, but differ on the outer whorls by the sparser ornament of *M. (M.) boulei* and also the strength of the lateral (2) tubercle in the latter as compared to that in *M. (M.) menabensis*. *M. (M.) cottreaui* has comparable ornament at similar stages, but has a much more compressed whorl section as compared to *M. (M.) boulei*. *M. (M.) lenoblei* has also been compared to the present species, and differs mainly in the effacement of ornament on the later whorls, especially towards the venter. Furthermore, the tubercles tend to be radially elongated. *M. (M.) dabolavaensis* is close to *M. (M.) boulei*, but generally has less strong, but denser ribbing. In addition, the ratio of external to internal tubercles in *M. (M.) dabolavaensis* is greater, there being up to three times as many external than internal tubercles.

### Occurrence

*Menabites (M.) boulei* is the index fossil for the uppermost Zone of the Lower Campanian in Madagascar. Zone of *M. boulei* and *Anapachydiscus arrialoorensis*, and thus allows for correct dating of locality 100 in Zululand which the authors previously (Kennedy & Klinger 1975: 295) had erroneously attributed to Lower Santonian.

*Menabites* s.l. sp. juv. indet.

Fig. 218B–C

### Material

SAM-PCZ5921 from the south-western shores of False Bay north of Nkundusi at locality 100, St Lucia Formation, Lower Campanian.

### Description and discussion

A fragment of a septate whorl and the corroded impression of a small *Menabites* may probably be referred to the subgenus *Australiella*. At a diameter of 10 mm the umbilical (1), ventrolateral (2, 3, 4) and external (5) tubercles are already prominently developed, and the keel appears entire. At 35 mm diameter, ornament consists typically of small, pointed umbilical (1) tubercles, very large nodose ventrolateral (2, 3, 4) tubercles and about two to three times as many obliquely elongated clavate external (5) tubercles. The keel is well developed and entire.



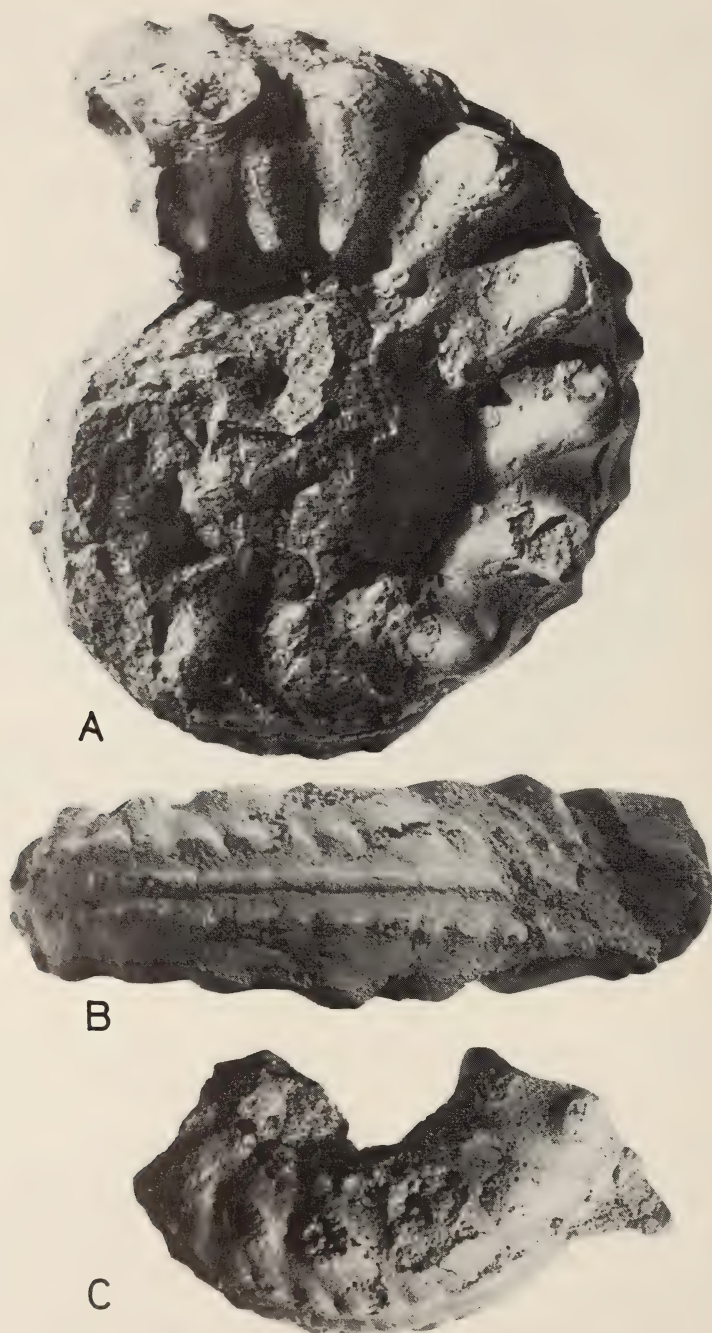


Fig. 218. A. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B. B-C. *Menabites* s.l. sp. juv. indet. SAM-PCZ5921.  $\times 1$ .

Specific identification of this fragment is impossible, but it is included to show the early trituberculate ornament. Similar juvenile specimens have been illustrated by Collignon (1948, pl. 7(1) (figs 8–9)) to illustrate the ontogenetic development of *Menabites*.

*Menabites (M.) boulei* occurs at the same locality and the inner whorls could possibly belong to that species.

#### Occurrence

Lower Campanian of Zululand.

#### *Menabites (Australiella) australis* (Besairie, 1930)

Figs 218A, 219–229, 230B, 231–240

*Mortoniceras australe* Besairie, 1930: 638, pl. 64 (fig. 2–2a).

*Mortoniceras cf. australe* Besairie, 1930: 638.

*Menabites (Australiella) australis* (Besairie): Collignon, 1948: 26, pl. 28 (fig. 1–1a).

*Australiella australis* (Besairie): Collignon, 1970: 54, pl. 630 (fig. 2326).

#### Type

Holotype is the specimen figured by Besairie (1930, pl. 64 (fig. 2–2a)) from the Campanian of Menabe, Madagascar.

#### Material

SAM-PCZ5898, Bed 3 locality 110, on the Nibela Peninsula, Zululand, St Lucia Formation, Campanian II; BMNH-C81475, C81478, Bed 4 at the same locality, Campanian III; SAM-PCP5689, SAS-Z191, Z705, Z1847, NMB-D1336A–D1336B, all from the same locality as SAM-PCZ5898 at various unrecorded horizons at this section; BMNH-C81476, C81482, C81485, locality 109, on the Nibela Peninsula, St Lucia Formation, Campanian II.

#### Dimensions

|                        | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>Lt</i> | <i>Ext.</i> |
|------------------------|----------|------------|------------|----------------|------------|-------------|-----------|-------------|
| PCZ5898                | 233,0    | 83,0(35,6) | 83,0(35,6) | 1,00           | 83,0(35,6) | 20          | 20        | 34          |
| D1336A                 | 100,0    | 53,0(53,0) | 34,0(34,0) | 1,56           | 41,0(41,0) | —           | 14        | 31          |
| at                     | 140,0    | 68,0(48,6) | 50,0(35,7) | 1,36           | 55,0(39,3) | 20          | 17        | 35          |
| at                     | 182,0    | 81,0(44,5) | 62,0(34,1) | 1,31           | 71,0(39,0) | 24          | 21        | 37          |
| D1336B                 | 86,0     | 48,0(55,8) | 34,0(39,5) | 1,41           | —          | —           | 15        | 29          |
| at                     | 120,0    | 64,0(53,3) | 52,0(43,3) | 1,23           | —          | —           | 16        | 31          |
| at                     | 147,0    | 78,0(53,1) | 67,0(45,6) | 1,16           | 51,0(34,7) | —           | 17        | 31          |
| Z705                   | 135,0    | 55,0(40,7) | 46,0(34,1) | 1,20           | 53,0(39,3) | —           | —         | —           |
| Z191                   | 196,0    | 80,0(40,8) | 65,0(33,2) | 1,23           | 76,0(38,8) | 22          | 21        | 39          |
| After Collignon, 1948: |          |            |            |                |            |             |           |             |
| I                      | 49       | 28(57)     | 22(45)     | 1,27           | 16(33)     | —           | —         | —           |
| II                     | 62       | 43(70)     | 27(44)     | 1,59           | 22(35)     | —           | —         | —           |
| III                    | 90       | 54(60)     | 42(70)     | 1,28           | 34(38)     | —           | —         | —           |
| IV (type)              | 92       | 56(61)     | 44(48)     | 1,27           | 35(38)     | —           | —         | —           |

#### Description

This species, as here interpreted, may grow to a very large size; one specimen, SAM-PCZ5898 (Figs 219–220), is still septate at a diameter of 315 mm.



Fig. 219. *Menabites (Australiella) australis* (Besairie, 1930). SAM-PCZ5898. Largest known specimen at 315 mm diameter, and still septate. Also shows transition from *Australiella* to *Menabites* or *Bererella* adult stage.  $\times 0,39$ .





Fig. 220. *Menabites (Australiella) australis* (Besairie, 1930). SAM-PCZ5898.  $\times 0,4$ .  
(See also Fig. 219.)

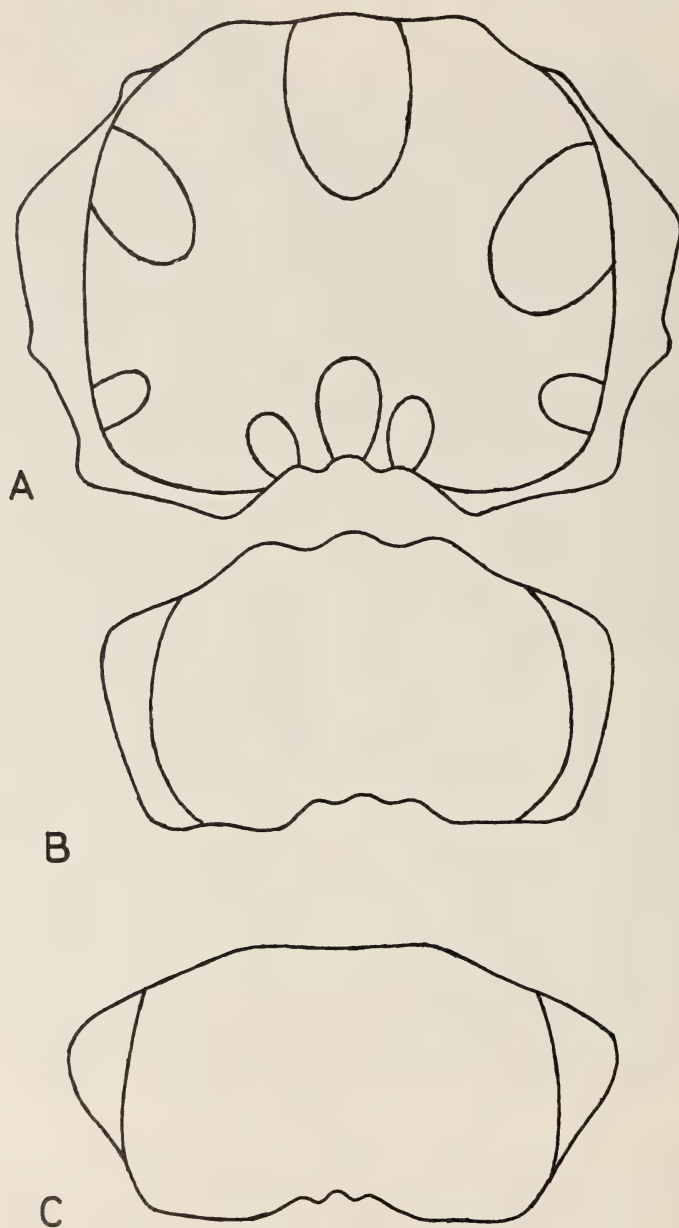


Fig. 221. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B.  
× 1. Changes in whorl section during ontogeny. (See also Figs 222–229.)

Coiling is relatively loose with an umbilical width of the order of 35 to 40 per cent of the diameter. The whorl section and details of ornament change continually through the ontogeny (Figs 221–229).

Unfortunately, none of the specimens has the very innermost whorls preserved, but at a diameter of *c.* 80 mm, the whorl section is already distinctly rectangular, much wider than high, with a very shallow dorsal zone of impression, little inflated, virtually parallel flanks and a slightly rounded venter (Fig. 227). Ornament at this stage consists of small, conical umbilical tubercles, connected in most cases by low, thick ribs to enormous bullate to spatulate ventrolateral nodes, which in turn are connected by very indistinct riblets to two or three rounded or obliquely elongated external tubercles. Some of the umbilical tubercles appear intercalatory, not being associated with any ribs. The keel is low and broad. Striking at these diameters are the enormous ventrolateral nodes and the curious, occasional intercalatory umbilical nodes.

With increasing diameter, the whorl section becomes more inflated, and the ventrolateral nodes become smaller and narrower and eventually show signs of division, giving rise to a new row of tubercles on the ventrolateral side. During this process, the lateral and ventrolateral tubercles tend to become absorbed in the ribs, which are now well defined. The diameter at which division of the ventrolateral tubercle into two takes place is variable, ranging from *c.* 120 mm in NMB–D1336B to 150 mm in NMB–D1336A.

Last to form is the lateral tubercle (2), dorsolaterally of the original ventrolateral spine. By this time the whorl section is well rounded, though still wider than high. With increasing diameter ribbing becomes bolder and tends to absorb the tuberculation to some extent.

The available specimens are all phragmocones, the largest being 315 mm in diameter. The suture has blocky saddles and lobes with minutely frilled elements (Fig. 231B).

### Discussion

The Zululand material is of extreme interest in showing virtually the whole ontogenetic development, changing from prominently trituberculate through quadrituberculate to pentatuberculate.

The authors are not entirely sure that their interpretation of the species is wholly correct, due to great differences in size between the Madagascar and Zululand specimens. It is not clear from Besairie's (1930: 638) or Collignon's (1948: 26–27, 1970: 54) descriptions of *M. (A.) australis* whether these specimens are still septate, or adult. The Madagascar specimens, if adults, are all very small, *c.* 80 mm–150 mm in diameter, when compared to the Zululand specimens, which are still septate at diameters in excess of 300 mm. The inner whorls of the Zululand specimens, with depressed, subrectangular whorl section and enormous ventrolateral spines are, however, like typical Madagascar *M. (A.) australis*. This raises the question of whether Madagascar *M. (A.) australis* which are, in fact, trituberculate throughout, have arisen caenogenetically from





Fig. 222. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B.  
Stage preceding that of Figure 223.  $\times 1$ .

a population similar to the much larger Zululand material, or whether this species has been interpreted only in terms of incomplete material in Madagascar. The holotype of *M. (A.) australis*, according to Besairie's figures, measures about 150 mm in diameter. None of the Zululand specimens is still unequivocally trituberculate at that diameter, although specimens such as NMB-D1336 (Fig. 229), with a very indistinct fourth row of tubercles, are very close to the holotype. Besairie (1930: 638) had referred to the Zululand material as *Mortoniceras* cf. *australis*, stating that it differed from *M. australis* only by the possession of a doubled row of tubercles in lieu of a single row.

In view of the normal wide range of intraspecific variation in the Texaninitinae, it is probably correct to refer the Zululand material to Besairie's species, and to regard the holotype of *M. (A.) australis* as an immature specimen.

Differences between *M. (A.) australis* and the majority of the other *M. (Australiella)* species described from Madagascar, e.g. *M. (A.) falloti*, *M. (A.) besairiei*, *M. (A.) subaustralis*, *M. (A.) moreti*, *M. (A.) antsirasiraensis*, *M. (A.) tintanti*, and *M. (A.) coronata* are difficult to formulate, as they seem

to grade into each other both in a vertical and in a lateral sense. The majority of these species occur at the same stratigraphic level in Madagascar, and differ mainly in details of whorl section and appearance or attenuation of ornament. In view of the normal wide range of intraspecific variation, the authors doubt if all these names should be retained.

*Australiella australis ingens* was separated by Collignon (1970: 62) from the nominate subspecies on the basis of the strong development of the ventro-



Fig. 223. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B. Stage following that of Figure 222, and preceding that of Figure 224.  $\times 1$ .



Fig. 224. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B. Stage following that of Figure 223, and preceding that of Figure 225.  $\times 0,9$ .





Fig. 225. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B.  
× 0,8.

lateral spines, the rounding of the venter and attenuation of the keel and external row of tubercles. None of the Zululand specimens shows this development and no data can be added.

Relationships with the closely allied *M. (A.) falloti* described below (p. 315) are not quite clear, but it seems that *M. (A.) falloti* grades upward in the exposures into *M. (A.) australis*. *M. (A.) falloti* has a more rounded whorl



Fig. 226. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336B. Lateral view of completely assembled specimen shown in Figures 222–225.  $\times 0,69$ .



Fig. 227. *Menabites (Australiella) australis* (Besairie, 1930). NMB-D1336A.  $\times 1$ .  
(See also Figs 218A, 228–229.)





Fig. 228. *Menabites (Australiella) australis* (Besairie, 1930).  
NMB-D1336A.  $\times 1$ .



Fig. 229. *Menabites (Australiella) australis* (Besairie, 1930).  
NMB-D1336A.  $\times 0,8$ .

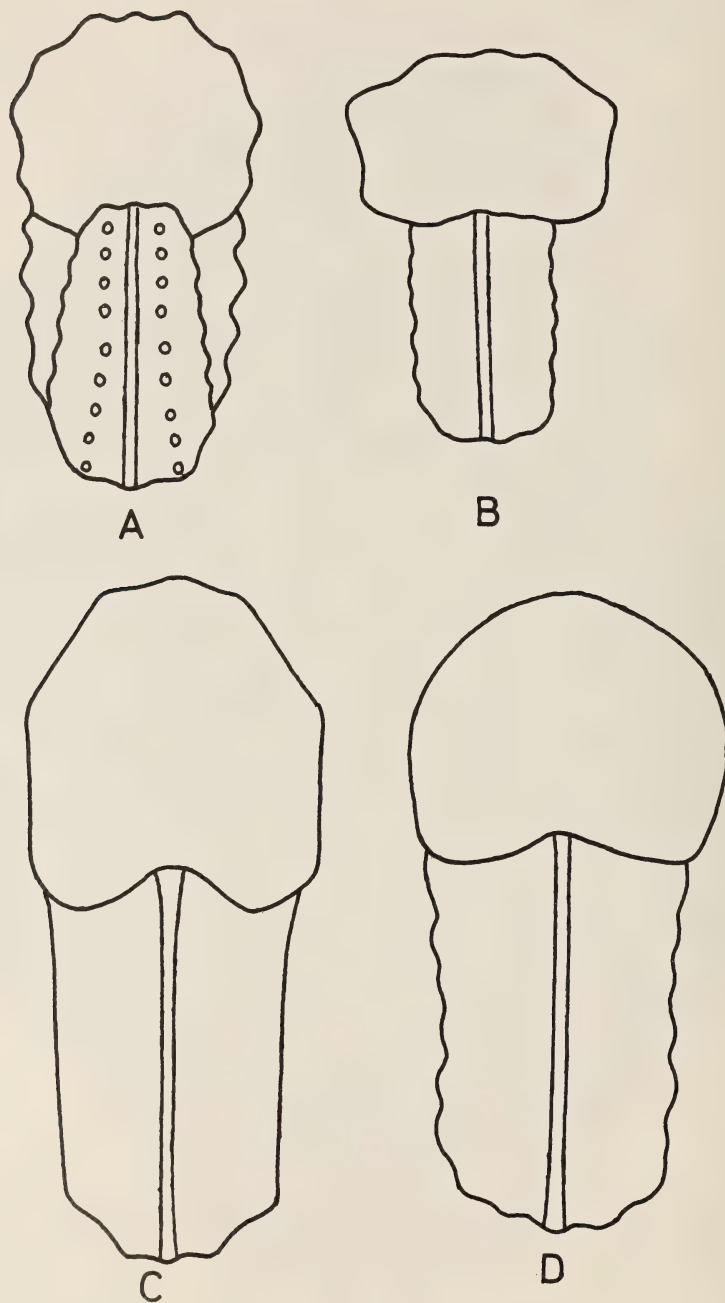


Fig. 230. *Menabites* (*Australiella*) species. Whorl sections. A. *M. (A.) falloti*. B. *M. (A.) australis*. C. *M. (A.) besairiei*. D. *M. (A.) moreti*.



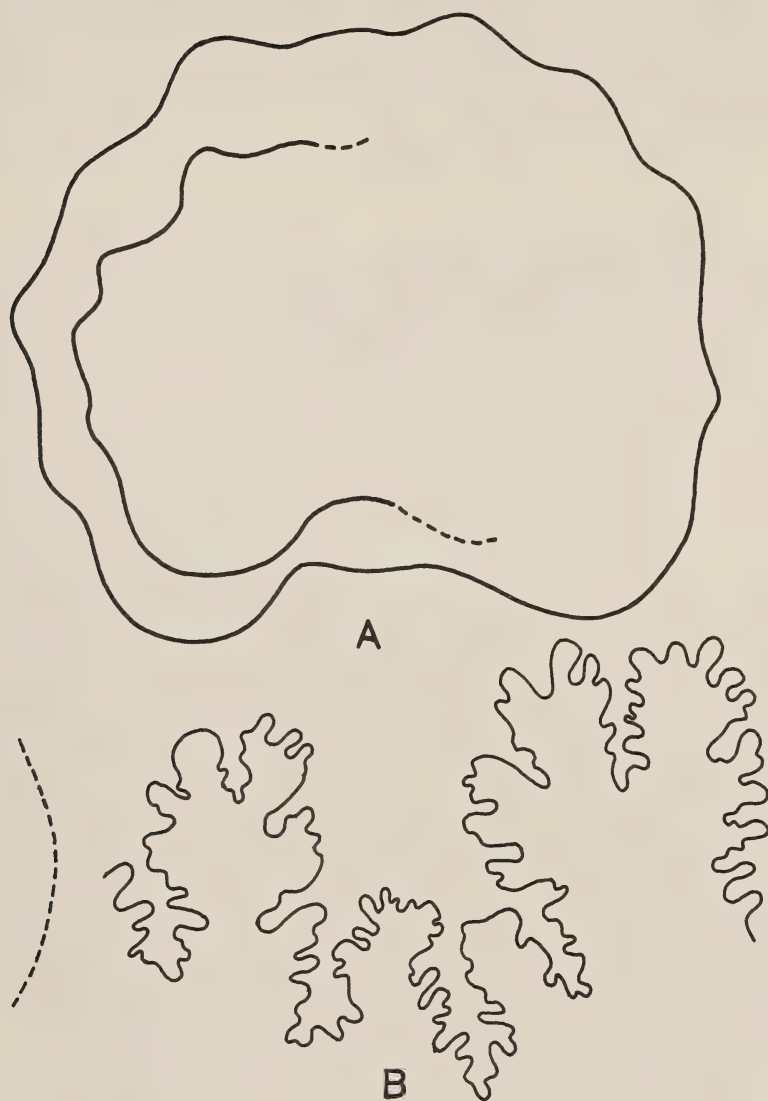


Fig. 231. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z1847. Showing whorl section and partial suture.  $\times 1$ .

section (Fig. 230A) and is pentatuberculate at a smaller diameter than *M. (A.) australis*. Single specimens each of *M. (A.) falloti*, *M. (A.) australis*, and *M. (D.) delawarensis* occur respectively in Beds 1, 2 and 3 at locality 110 (see Kennedy & Klinger 1975, fig. 9), suggesting that *M. (A.) australis* could be derived proterogenetically from *M. (A.) falloti*. Definite conclusions, however, must await more detailed collecting.

*M. (A.) tintanti* is a related species which also progresses beyond the tri-



Fig. 232. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z191. Specimen approximating the limits of *M. (A.) moreti* in being weaker ornamented and more rounded.  $\times 0.7$ .

tuberculate stage to quadrituberculate, and eventually pentatuberculate, though the lateral tubercle is weak. Dimensions of the holotype given below are virtually identical to the Zululand specimen NMB-D1336B at the same diameter.

|   | <i>D</i> | <i>Wb</i> | <i>Wb</i> | <i>Wb : Wh</i> | <i>U</i> |
|---|----------|-----------|-----------|----------------|----------|
| <i>M. (A.) tintanti</i> after Collignon . . . | 120      | 60(50)    | 47(39)    | 1,28           | 45(38)   |
| <i>M. (A.) australis</i> NMB-D1336B . . .     | 120      | 64(53)    | 52(43)    | 1,23           | —        |



Fig. 233. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z191. Specimen approximating the limits of *M. (A.) moreti* in being weaker ornamented and with a more rounded whorl section.  $\times 0,65$ .





Fig. 234. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z705. Specimen close to *M. (A.) coronata* due to depressed, coronate whorl section  $\times 1$ . (See Fig. 235A.)

Unfortunately, the holotype of *M. (A.) tintanti* was figured in lateral view only, but it seems to occupy a morphologically intermediate position between *M. (A.) falloti* and *M. (A.) australis*, in a sequence leading from a pentatuberculate stage through quadrituberculate to eventually trituberculate at comparable diameters. Given more material it would most probably be possible to include *M. (A.) tintanti* in the synonymy of one of the two species.

*M. (A.) subaustralis* has the same ornament and whorl section as *M. (A.) australis* at small diameters, but after 60 mm all ornament weakens, thus differing from the latter species.



Fig. 235. A. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z705. Specimen close to *M. (A.) coronata* due to depressed, coronate whorl section.  $\times 1$ . B. *Menabites (Delawarella) delawarensis* (Morton, 1831) SAS-Z2100.  $\times 0,72$ .



*M. (A.) besairiei* also seems somewhat transitional between *M. (A.) falloti* and *M. (A.) australis*, but has a distinct octagonal whorl section (Fig. 230C) compared to the rounded section of *M. (A.) falloti* or the rectangular depressed section of *M. (A.) australis*. Transitional forms such as SAM-PCZ5689 (Figs 239–240) and SAM-PCZ5685 (Fig. 241) connect the species.

*M. (A.) moreti* has inner whorls very much like *M. (A.) australis*, but has a



Fig. 236. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z1847.  $\times 0.8$ .





Fig. 237. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z2101.  $\times 0,84$ .

more rounded, narrower whorl section (Fig. 230D) than the latter, and has differently evolving ornament in that the ventrolateral spine weakens and becomes absorbed in the ribbing. SAS-Z191 (Fig. 232) is very much like *M. (A.) moreti*, in being more inflated and weaker ornamented than typical *M. (A.) australis*, pointing to the close relationship between the two species.

*M. (A.) antsirasiraensis* lacks the depressed whorl section and loses the ventrolateral spine at diameters between 70 and 80 mm.



Fig. 238. *Menabites (Australiella) australis* (Besairie, 1930). SAS-Z2102.  $\times 0.9$ .

*M. (A.) coronata* has a whorl section (Collignon 1970, pl. 631 (fig. 2328)) comparable to typical *M. (A.) australis* though not quite as depressed rectangular. Here the ventrolateral spines are not as strong and spatulate and about four external tubercles occur per spine. The whorl section of SAS-Z705 (Figs 234–235A) is virtually identical to that of the holotype of *M. (A.) coronata*, but it lacks the proliferation of external tubercles.



Fig. 239. *Menabites (Australiella) australis* (Besairie, 1930). SAM-PCZ5689. Transitional to *M. (A.) besairiei*.  $\times 0.6$ .





Fig. 240. *Menabites (Australiella) australis* (Besairie, 1930). SAM-PCZ5689. With whorl section transitional to *M. (A.) besairiei*.  
× 0,8.

*M. (A.) austinensis* was regarded as being close to *M. (A.) australis* by Young (1963), but was said to differ on account of having weaker ventrolateral clavae and stronger umbilical tubercles. These differences could all probably be incorporated in the intraspecific variation of *M. (A.) australis* as here interpreted, but the stratigraphic position of the species is perplexing. The species is based on two specimens, both with dubious locality data. Young (1963: 116), however, concludes that the species is either from 'Formation B or the Desau Chalk. Formation B seems the most likely. . . .' This would place the species in either Lower Santonian or Lower Campanian, probably Lower Santonian, and would be the oldest record of the subgenus. Until the question on the exact stratigraphic position is resolved, it is considered advisable to maintain the species apart from *M. (A.) australis*.

*M. (A.) pattoni* differs from *M. (A.) australis* in lacking the depressed whorl section in the early stages.

Retention of the trituberculate stage to a great diameter, and the presence of occasional intercalatory umbilical tubercles in *M. (A.) australis*, is very reminiscent of the situation as found in *Plesiotexanites matsumotoi* sp. nov. from the Middle Santonian of the Umzamba Formation. Apart from a more evolute mode of coiling in the latter, it also lacks the proliferation of external tubercles characteristic of *Menabites*. This seems to be just another example of heterochronous partial convergence with little genetic relationship.

#### Occurrence

Middle Campanian, Zone of *Delawareella subdelawarensis* and *Australiella australis* in Madagascar, and Campanian II–III of Zululand.

#### *Menabites (Australiella) falloti* (Collignon, 1932)

Figs 230A, 241–243

*Mortoniceras falloti* Collignon, 1932: 37, pl. 5 (fig. 1–1b); 1938: 76.

#### Type

The holotype is the specimen figured by Collignon (1932; pl. 5 (fig. 1–1b)) from the Senonian of Zululand, collected by P. Fallot in 1929 and presently housed in the Palaeontology Collections of the Geological Institute, Nancy.

#### Material

SAM-PCZ5870, Bed 1 locality 110, foreshore exposures at the south-western tip of Nibela, Zululand, St Lucia Formation, Campanian II; SAS-Z843, Z1547, Z2097, all from an unknown horizon at locality 109 or 110 at the south-western tip of the Nibela Peninsula, St Lucia Formation, Campanian II; BMNH-C81443–C81444, C81477, locality 109, St Lucia Formation, Campanian II.



Fig. 241. *Menabites (Australiella) falloti* (Collignon, 1932). SAM-PCZ5685. With whorl section transitional to *M. (A.) besairiei*.  
× 1.



*Dimensions*

|                          | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>L.</i> | <i>Ext.</i> |
|--------------------------|----------|------------|------------|----------------|------------|-------------|-----------|-------------|
| Holotype after Collignon | 90       | 34 (37,8)  | 35,0(38,9) | 0,97           | 30,0(33,3) | 22          | —         | —           |
|                          | 118,0    | 46,0(38,9) | 47,0(39,8) | 0,98           | 35,0(29,6) | 14          | —         | —           |
| Z843                     | 124,0    | 54,0(43,5) | 45,0(36,3) | 1,20           | —          | —           | —         | —           |
| Z2097                    | 176,0    | 63,0(35,8) | 61,0(34,7) | 1,03           | 58,0(32,9) |             |           |             |

*Description*

Coiling is moderately involute with an umbilical width of the order of 30 to 33 per cent of the total diameter. Whorl overlap is up to the fourth row of tubercles and the dorsal zone of impression is very shallow.

The whorl section is rounded, as wide as high in the early stages of growth (Fig. 243) but later becomes higher than wide (Fig. 230A); in some cases extremely so.

None of the Zululand specimens has the innermost whorls preserved, but at a diameter of *c.* 70 mm all five rows of tubercles are already present. These are: a conical umbilical (1) tubercle connected to a thickened rib which contains the second, third and fourth rows of tubercles, and of which the third row is most prominent. At the fourth row faint bifurcations become noticeable, ending in spirally elongated external (5) tubercles which protrude far beyond the venter on either side of a broad, weak central keel. In some cases it appears as if the bifurcations already originate at the third tubercle.

Ornament generally becomes stronger towards the later part of the phragmocone, but weakens again towards the body chamber.

The suture has broad saddles and lobes with minutely frilled terminations.

*Discussion*

This species is distinguished by the more or less rounded whorl section in the early stages of growth and by the early appearance of the pentatuberculate stage. Differences between *M. (A.) falloti* and *M. (A.) australis*, and even *M. (Delawareella) delawarensis* are gradational, as discussed above.

Subgeneric identity of the species is subjective. It may be argued that because of the relative early appearance of the pentatuberculate stage it should be referred to *Menabites* s.s. Because of the close resemblance to the holotype of the subgenus *M. (Australiella)*, however, it is here considered advisable to refer the species to subgenus *Australiella* rather than *Menabites* s.s. It may be noted here that Collignon also appeared to be in some doubt as to the subgeneric allocation in his 1948 monographic description of the Texanitinae. In comparing the species with *M. (A.) australis* (Collignon 1948: 27) he referred to it as *Menabites (Australiella) falloti*, but in his species list of the Texanitinae in the same volume (Collignon 1948: 44) refers it to *Bererella*.

Specimen SAS-Z843 (Figs 242–243) is closest to the holotype, which was most probably collected at the same locality by P. Fallot in 1929, during the Zululand excursion of the XV Session of the International Geological Congress.



Fig. 242. *Menabites (Australiella) falloti* (Collignon, 1932). SAS-Z843.  $\times 1$ .

Differences between *M. (A.) falloti* and *M. (A.) australis*, described above, are to be found mainly in the longer retention of the trituberculate stage and in the depressed rectangular whorl section of the latter species in the early stages.

Although sufficient precise stratigraphic data are not available, it appears possible to derive *M. (A.) australis* from *M. (A.) falloti* caenogenetically as discussed above.

Specimen SAM-PCZ5870 differs from the rest of the material in being much larger and in having a much more compressed section on the inner whorls, though the latter may be partially due to secondary crushing. Ornament on this specimen also weakens on the outer whorls, and may possibly connect



Fig. 243. *Menabites (Australiella) falloti* (Collignon, 1932). SAS-Z843.  $\times 1$ .



with *M. (Delawareella) gigas* sp. nov., described below.

SAM-PCZ5685 (Fig. 241) has inner whorls typical of *M. (A.) falloti*, but at a diameter of *c.* 180 mm, has an octagonal whorl section, very similar to that of *M. (A.) besairiei*. It is easily distinguished from the latter, however, on account of the early appearance of the pentatuberculate stage.

*M. (A.) tintanti* is a similar, large species, and was compared to *M. (A.) falloti* by Collignon (1970: 58); it differs mainly in retaining a quadrituberculate stage to a large diameter. SAS-Z2097 appears transitional to *M. (A.) tintanti* in having a very weakly developed lateral tubercle throughout and robust ribbing on the outer whorl. As discussed earlier, *M. (A.) tintanti* is intermediate between *M. (A.) falloti* and *M. (A.) australis*, and, given more material, may probably be synonymized with either of the two species.

The inner whorls of *M. (A.) falloti* resemble those of *M. (Delawareella) delawarensis*, which occurs at approximately the same stratigraphic level, and they may possibly be derived from a common ancestor. In larger specimens, however, *M. (Delawareella) delawarensis* is easily distinguished by the loss of lateral ornament.

#### Occurrence

Middle Campanian of Zululand and Madagascar, though apparently rare in Madagascar.

#### *Menabites (Delawareella) delawarensis* (Morton, 1830)

Figs 244–247A

*Ammonites delawarensis* Morton, 1830: 244, pl. 2 (fig. 4); 1834: 37, pl. 2 (fig. 5). Whitfield, 1892: 252, pl. 42 (figs 6–8).

*Mortonicerias delawarensis* (Morton): Weller, 1907: 837, pl. 103 (fig. 1). Grabau & Shimer, 1910: 227, fig. 1508.

*Menabites (Delawareella) delawarensis* (Morton): Collignon, 1948: 29. Reeside 1962: 131, pl. 72 (figs 1–3), pl. 73 (figs 1–5), pl. 74 (fig. 2).

*Delawareella delawarensis* (Morton): Young, 1963: 111, pl. 55 (fig. 5), pl. 61 (figs 1–6), pl. 63 (fig. 2), text-figs 15e, 20d, 25b, 26bfg, 27c, 29f.

#### Type

Holotype is the specimen figured by Morton (1830, pl. 2 (fig. 4)), housed in the Philadelphia Academy of Sciences.

#### Material

SAM-PCZ5905, Bed 3 locality 110, south-western tip of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian II; SAS-Z2097–Z2098, both from the same locality as above, but of unknown horizon. BMNH-C81438–C81439, locality 109, St Lucia Formation, Campanian II.

#### Dimensions

|       | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb : Wh</i> | <i>U</i>   | <i>Int.</i> | <i>L.</i> | <i>Ext.</i> |
|-------|----------|------------|------------|----------------|------------|-------------|-----------|-------------|
| Z2098 | 145,0    | 60,0(41,4) | 60,0(41,4) | 1,0            | 44,0(30,3) | 18          | 18        | 34          |
| Z2097 | 70,0     | 31,0(44,3) | 30,0(42,8) | 1,03           | 24,0(34,2) | —           | —         | —           |

*Description*

The material is not very well preserved, lacking the inner whorls, and finer details of ornament are obscured by crystalline matrix.

Coiling is moderately evolute, the umbilicus comprising 30 to 40 per cent of the diameter. The whorl section in all three specimens is virtually equidimensional hexagonal, with a near-vertical umbilical wall, flat flanks parallel up to the ventrolateral nodes on the inner whorls and then converging to a flattened venter (Fig. 247A).



Fig. 244. *Menabites (Delawarella) delawarensis* (Morton, 1830). SAS-Z2098.  $\times 1$ .



Fig. 245. *Menabites (Delawarella) delawarensis* (Morton, 1830). SAS-Z2098.  $\times 1$ .



On the inner whorls, ribs are feebly prorsiradiate up to the middle of the flanks where they pass through a large node, and then generally bifurcate and continue weakly up to the clavate external (5) nodes. At a diameter of *c.* 30 mm the ventrolateral node starts dividing into two on the ventral side, giving rise to a smaller clavate marginal (4) row of tubercles. The lateral (2) tubercles appear later, at *c.* 40 mm diameter, but these latter never really become prominent.

On the largest specimen, SAS-Z2098 (Fig. 244), the five rows of tubercles are spread out evenly over the flanks, and the submarginal (3) row is the most prominent, being distinctly pointed. Towards the larger end of this specimen tuberculation on the flanks weakens, and ribbing becomes dominant. The external tubercles, however, become stronger with increasing diameter and stand out as prominent serrate ridges. The keel, at this stage, shows low undulations corresponding in number to the external tubercles.

The suture is not well exposed in either of the specimens.

### Discussion

This species was discussed extensively by Reeside (1962) and Young (1963) and not much can be added to their comments.

The species is easily recognized by the very strong ornament when compared to other species of *M.* (*Delawareella*), and may in this respect be considered

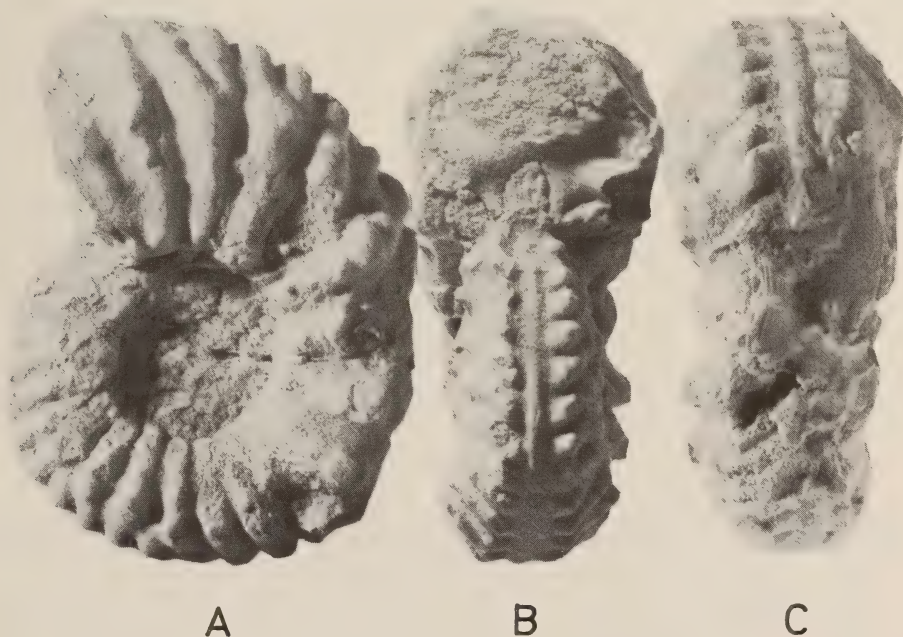


Fig. 246. *Menabites* (*Delawareella*) *delawarensis* (Morton, 1830). SAS-Z2097.  $\times 1$ .

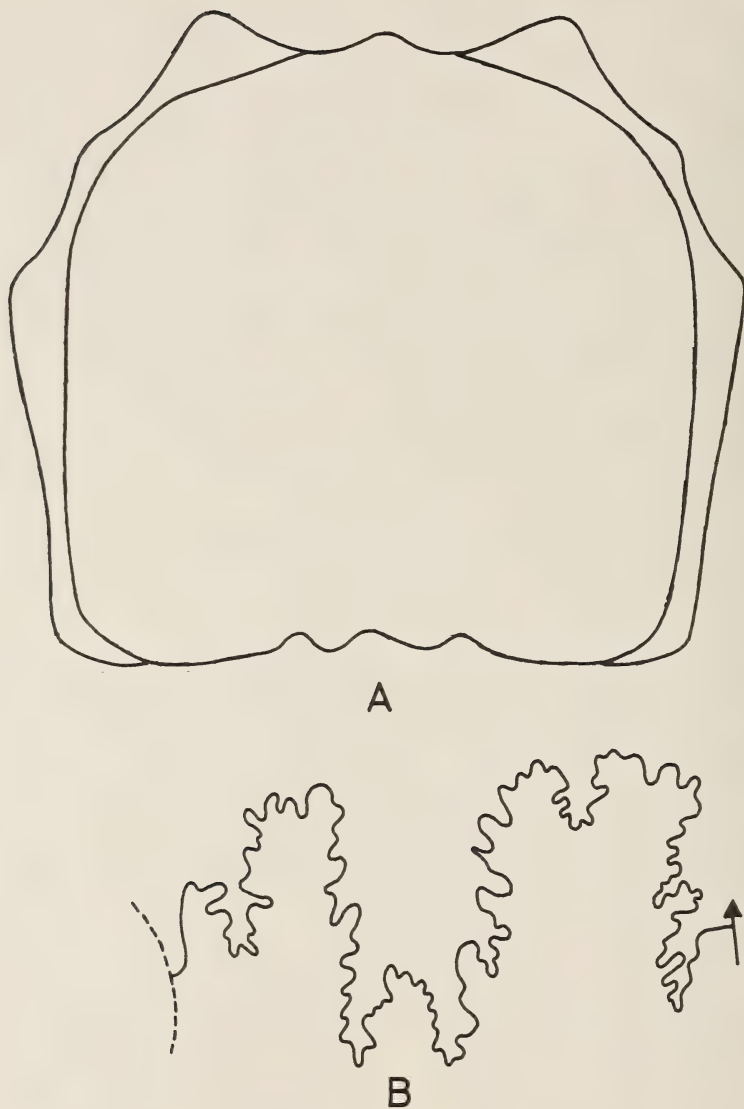


Fig. 247. A. *Menabites (Delawarella) delawarensis* (Morton, 1830). A. Whorl section of SAS-Z2907.  $\times 2$ . B. *Menabites (Delawarella) subdelawarensis* Collignon, 1948. Suture line of SAS-Z2100.  $\times 1$ .

transitional between *Menabites* s.s. and *M. (Delawarella)*.

*M. (Delawarella) roedereri* is similar in this respect in having strong ornament, but differs mainly in having a more compressed whorl section.

Collignon (1948: 32) separated *M. (Delawarella) subdelawarensis* (described below) as a Malagasy representative of this American species, differing mainly in having weaker ornament, and also a more compressed whorl section. These reasons appear sufficient for separation of the two species.

Unfortunately, none of the Zululand specimens has the body chamber preserved, but the magnificent specimen illustrated by Reeside (1962, pl. 74 (fig. 2)) shows the low, broad ribbing on the flanks.

### Occurrence

Campanian of Zululand, Gulf Coast region, and Delaware and New Jersey regions of North America.

### *Menabites (Delawarella) subdelawarensis* Collignon, 1948

Figs 247B–251

*Menabites (Delawarella) subdelawarensis* Collignon, 1948: 32, pl. 29 (figs 1–2).

*Menabites (Delawarella) subdelawarensis* var. *lenticularis* Collignon, 1948: 34, pl. 30 (fig. 1).

*Delawarella subdelawarensis* Collignon, 1970: 64, pl. 634 (fig. 2335).

### Type

Holotype is Collignon's (1948, pl. 29 (fig. 2)) specimen by original designation.

### Material

SAM-PCZ5901, Bed 3 locality 110, south-western tip of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian III; SAS-Z2100 from an unknown horizon at the same locality; BMNH-C81443–C81444, locality 109, St Lucia Formation, Campanian II.

### Dimensions

|         | <i>D</i> | <i>Wh</i>   | <i>Wb</i>   | <i>Wb : Wh</i> | <i>U</i>      | <i>Int.</i> | <i>L.</i> | <i>Ext.</i> |
|---------|----------|-------------|-------------|----------------|---------------|-------------|-----------|-------------|
| Z2100   | 221,0    | 84,0(38,0)  | 103,0(46,6) | 0,81           | 59,0(26,7)    | 23          | —         | —           |
| PCZ5901 | 340,0    | 119,0(35,0) | 155,0(45,6) | 0,76           | c.110,0(32,4) | —           | —         | 42          |

### Description

Unfortunately, the specimens are in a poor state of preservation, but partially permit examination of specific characteristics.

The umbilical width of the very large specimen, SAM-PCZ5901 (Figs 248–250), which is still septate at the larger end, is probably a little too large due to fracture of the last part of the whorl. An umbilical width of 26 per cent as in the smaller specimen seems more realistic. The whorl section is massive





Fig. 248. *Menabites (Delawareella) subdelawarensis* Collignon, 1948. SAM-PCZ5901. Gigantic specimen still fully septate.  $\times 0,34$ .

throughout, higher than wide, with a dorsal zone of impression which embraces preceding whorls up to the lateral tubercle, and a vertical to inward or outward sloping umbilical wall merging abruptly with the flanks, which remain parallel up to the lateral tubercle at about midflank, and then converge obliquely to a very broad venter.

In SAS-Z2100 (Fig. 251) the typical *Menabites* trituberculate ornament is still visible at a diameter of about 40 mm, but thereafter very quickly becomes pentatuberculate and rather weak. Ornament after that consists of relatively weak ribs bifurcating occasionally at the umbilical edge, each bearing five



Fig. 249. *Menabites (Delawareella) subdelawarensis* Collignon, 1948. SAM-PCZ5901. Gigantic specimen still fully septate. Opposite lateral view of Fig. 248.  $\times 0,34$ .

rows of tubercles of which the umbilical (1) and external (5) ones are strongest. The lateral (2) tubercles are very weak, and the submarginal (3) and marginal (4) ones only slightly stronger. All five rows of tubercles are spaced equidistantly over the flanks.

In this smaller specimen, SAS-Z2100 (Fig. 251), ribs become bolder and more widely spaced at the largest diameter, whilst the whorl section also appears to become more inflated. In the larger specimen, SAM-PCZ5901 (Figs 248–250), all ornament weakens at the largest diameter with no distinct strengthening of the ribs.





Fig. 250. *Menabites (Delawarella) subdelawarensis* Collignon, 1948. SAM-PCZ5901. Gigantic specimen still fully septate.  $\times 0,46$ . (See also Figs 248–249.)





Fig. 251. *Menabites (Delawareella) subdelawarensis* Collignon, 1948. SAS-Z2100.  $\times 0,63$ .

The keel throughout is broad and low, and eventually becomes very indistinct at large diameters.

The suture line is blocky with minutely frilled terminations, though details are somewhat obscured by weathering and calcitic encrustation (Fig. 247B). The lateral lobe (L) in SAS-Z2100 is wide and asymmetrically trifid, and deeper than the external lobe.

### Discussion

Comparison of the Zululand material with that described from Madagascar by Collignon (1948, 1970) is difficult due to great differences in size, the largest described specimen from Madagascar (Collignon 1970: 68) being only 166 mm in diameter compared to the smallest Zululand specimen at 221 mm diameter. Nevertheless, the massive whorls, and generally coarse ornament of the Zululand specimens compare well with the Madagascar material.

The closest ally to *M. (D.) subdelawarensis* is undoubtedly *M. (D.) jeanneti*, which also occurs in two forms; a normally inflated form and a compressed form. Major differences between the two species according to Collignon (1948: 36) are that the whorls of *M. (D.) jeanneti* are less massive, the ribs straighter, finer and denser, and the lateral lobe (L) is bifid instead of trifid.

The Zululand material seems to suggest that *M. (D.) jeanneti* could possibly be derived from *M. (D.) subdelawarensis* through tighter coiling and proliferation of ribbing, but unfortunately insufficient material is as yet available to fully substantiate this assumption.

The inner whorls of the larger specimen, SAM-PCZ5901 (Figs 248–250), are remarkably like those of *M. (D.) gigas* sp. nov. which occurs at a slightly lower stratigraphic level at the Nibela Peninsula, but in the latter increase in whorl size is much more rapid.

### Occurrence

Campanian III of Zululand, and the Mid-Campanian Zone of *Delawarella subdelawarensis* and *Australiella australis* of Madagascar.

*Menabites (Delawarella) sp. aff. jeanneti* s.l. Collignon, 1948

Figs 252–255

Compare:

*Menabites (Delawarella) jeanneti* Collignon, 1948: 34, pl. 30 (fig. 3–3b) pl. 31 (fig. 1–1b).

*Menabites (Delawarella) jeanneti* var. *compressa* Collignon, 1948: 36, pl. 31 (fig. 2–2a).

*Delawarella jeanneti* Collignon: Collignon, 1970: 64, pl. 634 (fig. 2336).

### Dimensions

|         | D     | Wb         | Wh         | Wb : Wh | U          | Int. | L. | Ext. |
|---------|-------|------------|------------|---------|------------|------|----|------|
| PCZ5691 | 143,0 | 56,0(39,2) | 68,0(47,6) | 0,82    | 36,0(25,2) | 23   | —  | —    |

### Material

SAM-PCZ5691, Bed 7 locality 110, south-western tip of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian III; and SAM-FB from the collection of S. H. Haughton from an unknown horizon and locality in the False Bay region of Zululand, but probably the same locality as above.



Fig. 252. *Menabites (Delawareella)* sp. aff. *jeanneti* s.l. Collignon, 1948. SAM-PCZ5691.  $\times 0,78$ .

### *Description*

Coiling is involute with an umbilical diameter of about 25 per cent. The whorl section is compressed with a prominent dorsal zone of impression, a vertical to overhanging umbilical wall with a well-defined umbilical edge and weakly inflated flanks with maximum width at the site of the lateral tubercle.

None of the specimens has the innermost whorls preserved, but at a diameter of 45 mm ornament is already very much weakened with barely perceptible lateral and submarginal tubercles. The umbilical tubercles are radially





Fig. 253. *Menabites* (*Delawarella*) sp. aff. *jeanneti* s.l. Collignon, 1948. SAM-PCZ5691.  
 $\times 0,85$ .

elongated and point strongly inward. With increasing diameter ribbing remains weak and prorsiradiate with barely perceptible lateral (2) and submarginal (3), and slightly stronger marginal (4), but progressively stronger umbilical (1) and external (5) tubercles. Numerous intercalations and bifurcations occur, generally at the site of the submarginal tubercle, but also occasionally at the umbilical tubercle. This results in there being about twice as many external as internal tubercles.

Specimen SAM-PCZ5691 (Figs 252-253) has part of the early body chamber preserved. Here tuberculation weakens even more, and the ribs become wider spaced.

The suture is only partially exposed in the present material. The keel, as far as can be seen, is never very prominent.



Fig. 254. *Menabites* (*Delawarella*) sp. aff. *jeanneti* s.l. Collignon, 1948. SAM-FB.  $\times 1$ .

*Discussion*

This species is identified by the fine, dense ribbing throughout, and the very poor development of the lateral and submarginal tubercles.

Collignon (1948: 34–36), in erecting *M. (D.) jeanneti*, distinguished between a typical form and a more compressed form, var. *compressa*, the difference in whorl breadth between the two forms being approximately 5 per cent. The larger Zululand specimen, SAM-PCZ5691 (Figs 252–253), with a whorl breadth of 39 per cent of the diameter, appears closer to the typical form of *M. (D.) jeanneti* than to the compressed variety. The main difference between the Zululand material and the Malagasy specimens of *M. (D.) jeanneti*, lies in the fact that, in the adult stage, the latter lose ornament on the venter and take on the appearance of a pachydiscid. In the Zululand specimens the venter remains



Fig. 255. *Menabites (Delawarella)* sp. aff. *jeanneti* s.l. Collignon, 1948. SAM-FB.  $\times 1$ .



more or less flat, and the external tubercles are prominent, hence it is advisable to refer to the material as *M. (D.)* sp. aff. *jeanneti* rather than a definite reference.

The specimen described below as *M. (Delawarella)* sp. indet. has similar weak ornament on the flanks, but lacks the strong development of the umbilical and external tubercles, and, in addition, has a distinct crenulate keel.

*M. (Delawarella) nibelae* sp. nov. (discussed below) differs from the present species in being slightly more narrowly umbilicate and in having a more inflated whorl section.

The closest ally to the present species is *M. (D.) subdelawarensis*, from which it is possibly derived through slight reduction of umbilical width, compression of the whorls and fining of ornament.

Other species of *M. (Delawarella)* such as *M. (D.) gigas* sp. nov. and *M. (D.) delawarensis*, all differ on account of the much more prominent ornament.

#### Occurrence

Campanian of Zululand; in the Mid-Campanian Zone of *Delawarella subdelawarensis* and *Australiella australis* of Madagascar.

#### *Menabites (Delawarella) gigas* sp. nov.

Figs 256–258

#### Holotype

SAM-PCZ5900 (Fig. 256), Bed 1 locality 110, south-western tip of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian II.

#### Etymology

Pertaining to great size.

#### Material

SAS-Z1951 and SAS-A1867, both from the same locality as the holotype but from an unknown horizon, can also be referred to this species.

#### Dimensions

|         | <i>D</i> | <i>Wb</i> | <i>Wh</i> | <i>Wb : Wh</i> | <i>U</i>  |
|---------|----------|-----------|-----------|----------------|-----------|
| PCZ5900 | c.700    | —         | c.270(37) | —              | c.240(34) |

#### Description

Unfortunately none of the specimens has the very innermost trituberculate whorls preserved. Coiling is involute, with a very rapid increase in whorl size, and an umbilical width of the order of 30 to 35 per cent of the total diameter. The whorl section throughout is higher than wide, but is more inflated on the phragmocone than on the body chamber. The umbilical wall is vertical to overhanging.

Ornament on the phragmocone is basically of the *Menabites* type, very



Fig. 256. *Menabites (Delawarella) gigas* sp. nov. Holotype SAM-PCZ5900.  $\times 0,23$ .  
Scale bar in millimetres.

reminiscent of *M. (Australiella) falloti* (see p. 315), which occurs at the same stratigraphic level. Ornament here consists of low, single ribs, each bearing a distinct umbilical (1) tubercle, but low, rounded and indistinct lateral (2), submarginal (3), and marginal (4) tubercles.

The body chamber, which is partially preserved on the holotype (Fig. 256) and SAS-Z1951 (Fig. 257), is enormous, comprising at least half a whorl. All lateral ornament is here effaced, and on the holotype this even affects the umbilical tubercles.

The suture is imperfectly known, but includes a very wide, asymmetric bifid lobe (L) (Fig. 258).



Fig. 257. *Menabites (Delawarella) gigas* sp. nov. Paratype SAS-Z1951.  $\times 0,45$ .



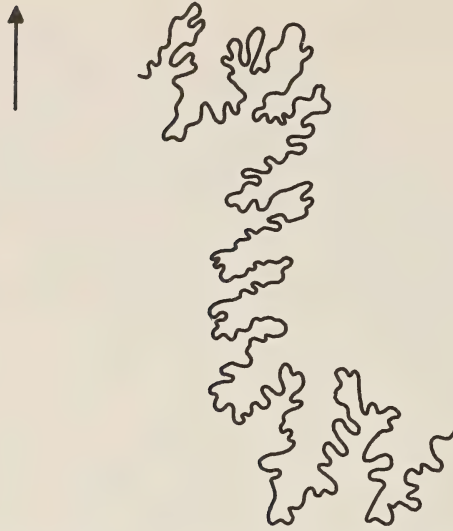


Fig. 258. *Menabites (Delawarella) gigas* sp. nov. Paratype SAS-Z1951. Showing partial suture.  $\times 0,95$ .

### Discussion

This species is very easily recognized by virtue of its large size, lateral compression and complete lack of ornament on the body chamber.

The inner phragmocone whorls are very similar to those of *M. (Australiella) falloti*, and the holotype of the species was recovered from the same horizon (Bed 1 locality 110) as *M. (A.) falloti*, specimen SAM-PCZ5870. This seems to indicate that, at that particular stratigraphic interval, *Menabites (Australiella)* and *M. (Delawarella)* had already evolved into two distinct lineages. It is also interesting to note the very large size of the Zululand specimen. This, to the authors' knowledge, is the largest texanitid recovered so far.

*M. (D.) jeanneti* resembles *M. (D.) gigas* in losing virtually all texanitid ornament on the outer whorls (see Collignon 1948, pl. 31 (fig. 1-1b)), but differs in having a more inflated whorl section.

*M. (D.) subdelawarensis*, another species known to grow to enormous size in Zululand (p. 325), also differs in having a more inflated whorl section and generally much finer ornament.

*M. (A.) australis*, which may also grow to enormous size, is easily distinguished by the long persistence of the trituberculate stage and also by the more robust ornament.

The very large body chamber compared to the relatively small phragmocone indicates that buoyancy control in this species must have been very delicate.

### Occurrence

Campanian II of Zululand.

*Menabites (Delawarella) nibelae* sp. nov.

Figs 259–261

*Holotype*

SAS-Z2101 (Figs 259–261), locality 110, south-western tip of the Nibela Peninsula, Zululand, St Lucia Formation, probably Campanian III.

*Etymology*

Named after the Nibela Peninsula at the northern side of Hell's Gates, connecting False Bay to Lake St Lucia.

*Material*

Only the holotype.

*Dimensions*

|       | <i>D</i> | <i>Wb</i>  | <i>Wh</i>  | <i>Wb: Wh</i> | <i>U</i>   | <i>Int</i> | <i>L</i> | <i>Ext</i> |
|-------|----------|------------|------------|---------------|------------|------------|----------|------------|
| Z2101 | 164,0    | 67,0(40,8) | 81,0(49,4) | 0,83          | 37,0(22,6) | 25         | 25       | 39         |

*Description*

Coiling is involute, with a very narrow umbilicus, measuring only 22 per cent of the total diameter. The whorl section in the adult stage is higher than wide (Fig. 261) with a vertical umbilical wall, and little inflated flanks converging to a rounded venter. Inflation of the whorl increases with increasing diameter.

Where visible, ornament is subdued throughout, and consists of small radially elongated umbilical (1) tubercles, a hardly visible lateral (2) and submarginal (3) tubercle, poorly developed marginal (4) tubercle but prominent external (5) tubercles, all situated on poorly developed radial to prorsiradiate ribs. The ribs may be single, but the majority generally bifurcate at the submarginal tubercle or arise as intercalatories at the marginal tubercles, giving rise to many more external than internal tubercles. The keel is initially broad and strong, but becomes indistinct towards the later part of the phragmocone and on the body chamber.

*Discussion*

This species combines some of the characteristics of *M. (D.) delawarensis*, *M. (D.) subdelawarensis* and *M. (D.) jeanneti*, pointing to the close relationship between the various species.

The wide spacing of ribbing on the outer whorls is reminiscent of *M. (D.) delawarensis*, the whorl section is that of *M. (D.) subdelawarensis*, whereas the virtual absence of lateral (2) and submarginal (3) tubercles is reminiscent of *M. (D.) jeanneti*. There is certain resemblance to the specimen described below as *M. (D.)* sp. indet. (p. 342), but in the latter the whorl section is more inflated at comparable diameters, and the keel is crenulate, compared to entire in the present species.



Fig. 259. *Menabites (Delawarella) nibelae* sp. nov. Holotype SAS-Z2101.  $\times 0,88$ .

This is the *M. (Delawarella)* species with the narrowest umbilical width, the next tightly-coiled species being *M. (Delawarella) jeanneti* with an umbilical width of 24 to 29 per cent compared to 22 per cent in the former. Examination of the whorl sections of the two species and details of ornament over the venter at comparable diameters (see Collignon 1948, pl. 30 (fig. 3), pl. 31 (fig. 1)) clearly shows the differences. The whorl section of *M. (D.) jeanneti* is much





Fig. 260. *Menabites (Delawareella) nibelae* sp. nov. Holotype SAS-Z2101.  $\times 0,94$ .

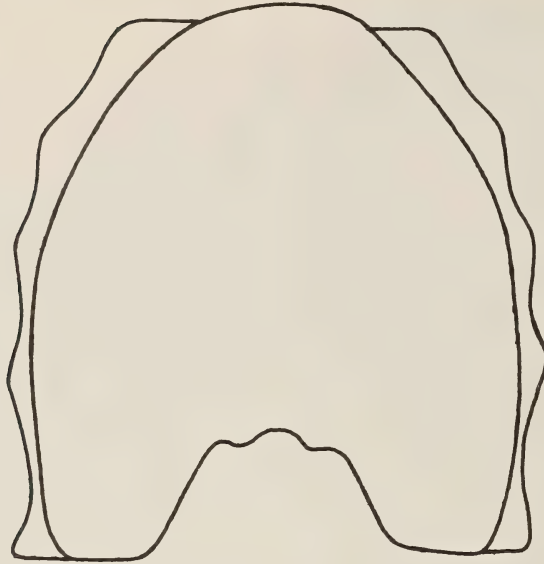


Fig. 261. *Menabites (Delawarella) nibelae* sp. nov. Holotype SAS-Z2101.  
Showing whorl section.  $\times 1$ .

more compressed, and at larger diameters tends towards weakening of the external tubercles over the venter.

The exact horizon from which this specimen was collected at locality 110 is not known, but as far as the authors can recall, it was found high up in the sequence, above the level of abundant menabitids. This could possibly indicate yet another trend towards recoiling in the texanitids, possibly starting with a relatively evolute form such as *M. (A.) falloti* through *M. (Delawarella) jeanneti* to the present species.

#### *Occurrence*

Campanian of Zululand.

*Menabites (Delawarella)* sp. indet.

Fig. 262

#### *Material*

SAM-PCZ5692, locality 110, south-western tip of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian II.

#### *Description*

A single septate specimen consisting of approximately a quarter of a whorl is referable to *M. (Delawarella)*, although specific identification is not possible.

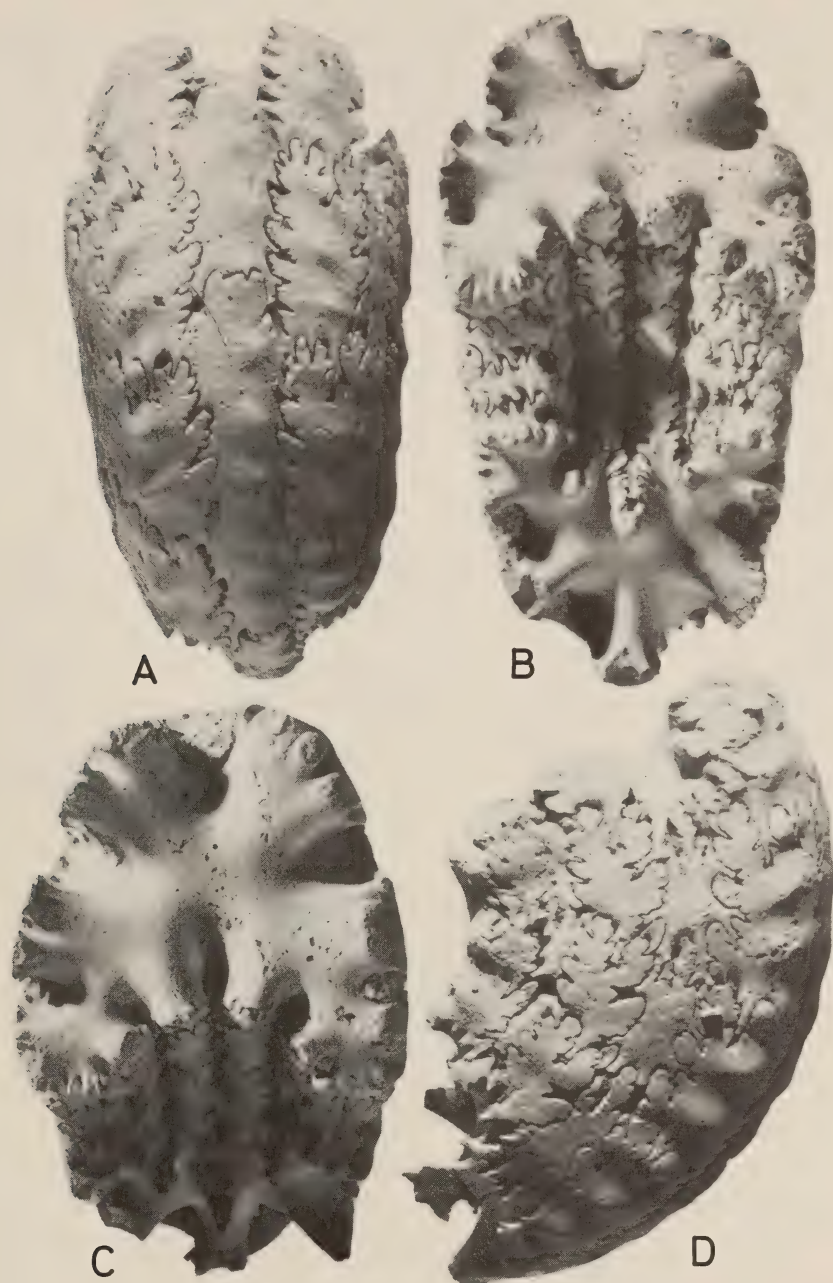


Fig. 262. *Menabites (Delawareella)* sp. indet. SAM-PCZ5692.  $\times 1$ .



The whorl section is ovoid, wider than high with a prominent dorsal zone of impression, a vertical umbilical wall and gently rounded flanks converging to a broadly rounded venter. The keel is broad and low, and distinctly undulating, though it is not quite clear if the undulations correspond to the external tubercles.

Save slight undulations, all lateral ornament is absent, with only umbilical (1) and external (5) tubercles present. The umbilical nodes are rounded to slightly radially elongated. The external tubercles are clavate and obliquely aligned in a forward direction. The ratio of external to umbilical tubercles is of the order of three to one.

The suture is beautifully exposed as seen in Figure 262.

### *Discussion*

Despite the fragmentary nature of this specimen, it differs from all known Zululand specimens on account of the broad, undulating keel and rapid loss of lateral ornament.

*M. (Delawarella) subdelawarensis* (see especially Collignon 1948, pl. 29 (fig. 1)) has a comparable whorl section, but lacks the undulating keel and strong attenuation of ornament. *M. (Delawarella) delawarensis* has an undulating keel in later stages of growth, but is easily distinguished on account of the strong ornament. *M. (Delawarella) jeanneti* is also somewhat similar in attenuation of lateral ornament, but has a more compressed whorl section at a comparable diameter (see Collignon 1948, pl. 30 (fig. 3)).

Hopefully further collection will permit definite identification of this species.

### *Occurrence*

Campanian II of Zululand.

## Genus *Spinptychus* Trauth

Figs 263–265

### *Type species*

*Aptychus spinosus* Cox, 1926.

### *Description and discussion*

The association of the aptychus form-genus *Spinptychus* Trauth with the genus *Texanites* was discussed on an earlier occasion by the authors (Kennedy & Klinger 1972: 394–399; Klinger 1972: 105–109). Two texanitine specimens, one of them referred tentatively to *Texanites soutoni*, were available to the authors, and it was concluded that the association of *Spinptychus* with *Texanites* is real. Since then, three more aptychi have been found, either in body chambers of, or associated with, texanitids, thus further establishing the relationship between *Spinptychus* and Texanitinae.

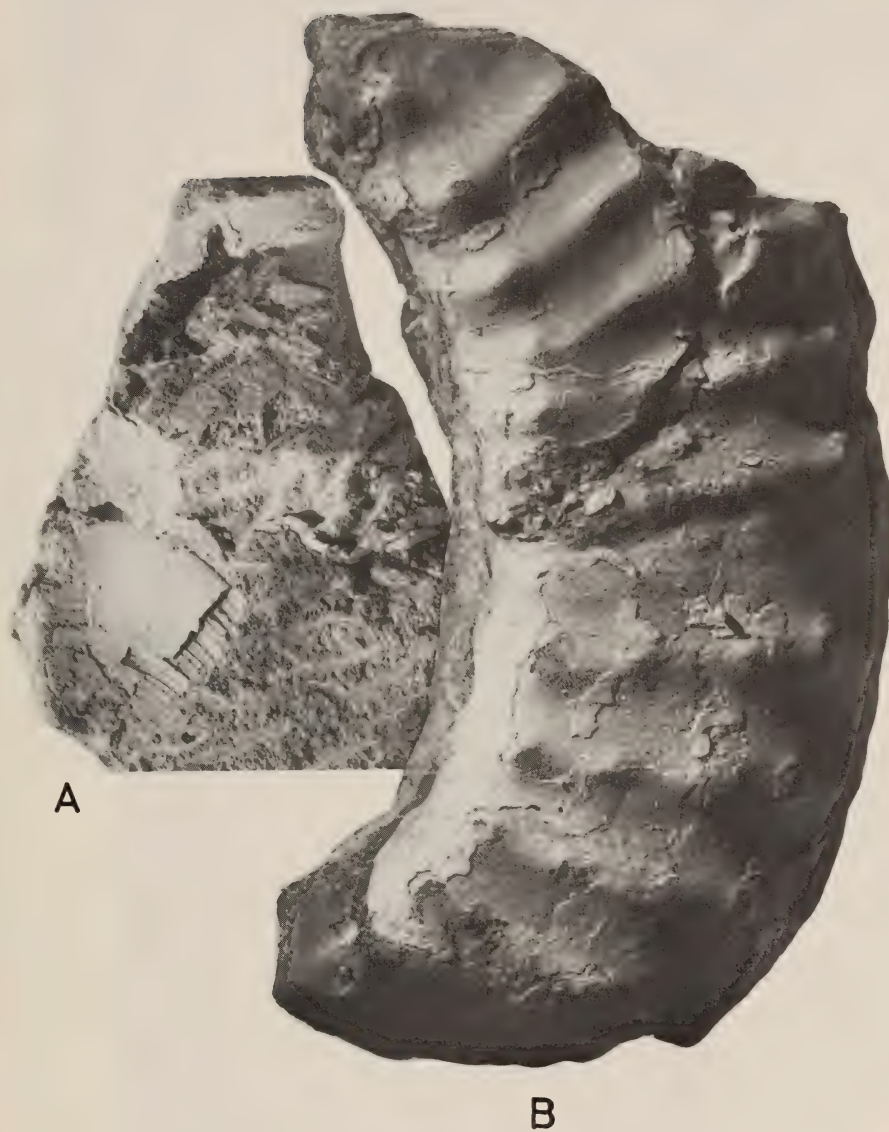


Fig. 263. *Spinptychus*. SAM-K5551. Fragment of *Spinptychus* in body chamber of *Plesiotexanites stangeri*.  $\times 1$ .

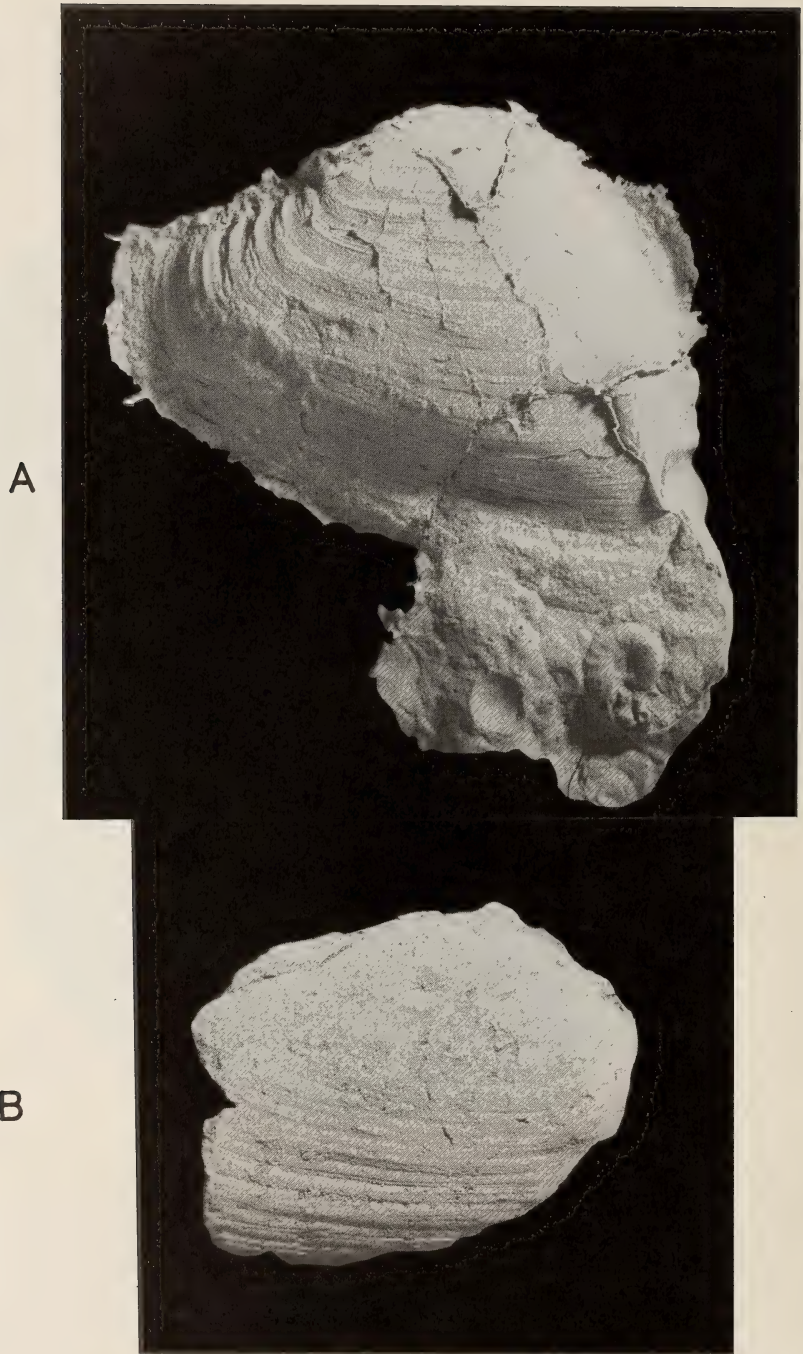


Fig. 264. *Spinaptychus*. A. Silicone rubber mould of SAM-PCZ5876 (see Fig. 265).  
B. SAM-PCZ5875.  $\times 1$ .





Fig. 265. *Spinaptychus*. SAM-PCZ5876. In body chamber fragment of *Texanites soutoni natalense* ssp. nov.  $\times 1,15$ .

SAM-K5551 (Fig. 263), from locality 1 at Umzamba Cliff, Pondoland, is a body chamber fragment of *Plesiotexanites stangeri* with part of one valve of the aptychus preserved. The concentric striae clearly point to *Spinaptychus*.

SAM-PCZ5875 (Fig. 264B) is a complete internal mould of the right valve of a *Spinaptychus* from the Santonian/Campanian of locality 6 at the Enseleni Reserve. The accompanying ammonoid fauna consists predominantly of *Pseudoschloenbachia umbulazi*, *Hauericeras gardeni* and *Texanites* gr. ex. *soutoni*, and *Plesiotexanites stangeri*. Of these, only *T. soutoni* is large enough to accommodate such a large aptychus.

SAM-PCZ 5876 (Fig. 265) is a virtually complete internal mould of the right valve of a *Spinaptychus* in the body chamber of *Texanites soutoni natalense*, from the Upper Santonian/Lower Campanian sediments at locality 105 on the south-eastern shores of False Bay.

Unfortunately none of the specimens is sufficiently preserved for detailed studies, but the sheer size and relative position of the aptychi still lead the authors to regard *Spinaptychus* as possibly an operculum as well as a jaw-apparatus as has been suggested for some uncalcified forms, especially anaptychi (see Lehmann 1967, 1970, 1971, 1972, 1975).

*Spinaptychus* is now definitely known to occur with *T. soutoni* and *P. stangeri*. As *T. soutoni* is transitional to *Submortonicer*, it is to be expected that the latter genus also bears spinaptychi.

## EVOLUTION AND EVOLUTIONARY TRENDS IN TEXANITINAE

Details of the suggested evolution of the Texanitinae as indicated by the South African material, and discussed in various sections of the systematic descriptions, are outlined in Figure 266. These differ somewhat from Matsumoto's (1955, 1965, 1970), Collignon's (1948), and Young's (1963) ideas, but should be seen as complementary to their findings rather than revolutionary.

The origin of the Texanitinae is still not resolved. The earliest genus appears to be *Protexanites* s.s., but data on the origin of the latter appear conflicting. Matsumoto (1955: 39, 1970: 230) favours deriving *Protexanites* s.s. from *Subprionocyclus*, and the authors concur in the case of species such as *P. bontanti*, *P. canaensis*, and *P. cyni*, but have their doubts in the case of more evolute, coarser-ornamented species such as *P. bourgeoisi* and *P. shoshonense*. Some of the South African material seems to suggest that it would be possible to derive *Paratexanites* via *Protexanites*, or both, from the aberrant Peroniceratid '*Fraudatoroceras*', but more material is needed to solve this problem satisfactorily.

The root of texanitine radiation in South Africa appears to lie in *Paratexanites*, especially the species *P. australis*, *P. pseudotricarinatum*, and *P. umkwelanense*. Thus, from these, *Protexanites* (*Pleurotexanites*), *Plesiotexanites*, and probably also part of *Texanites* s.s. may be derived. It is possible

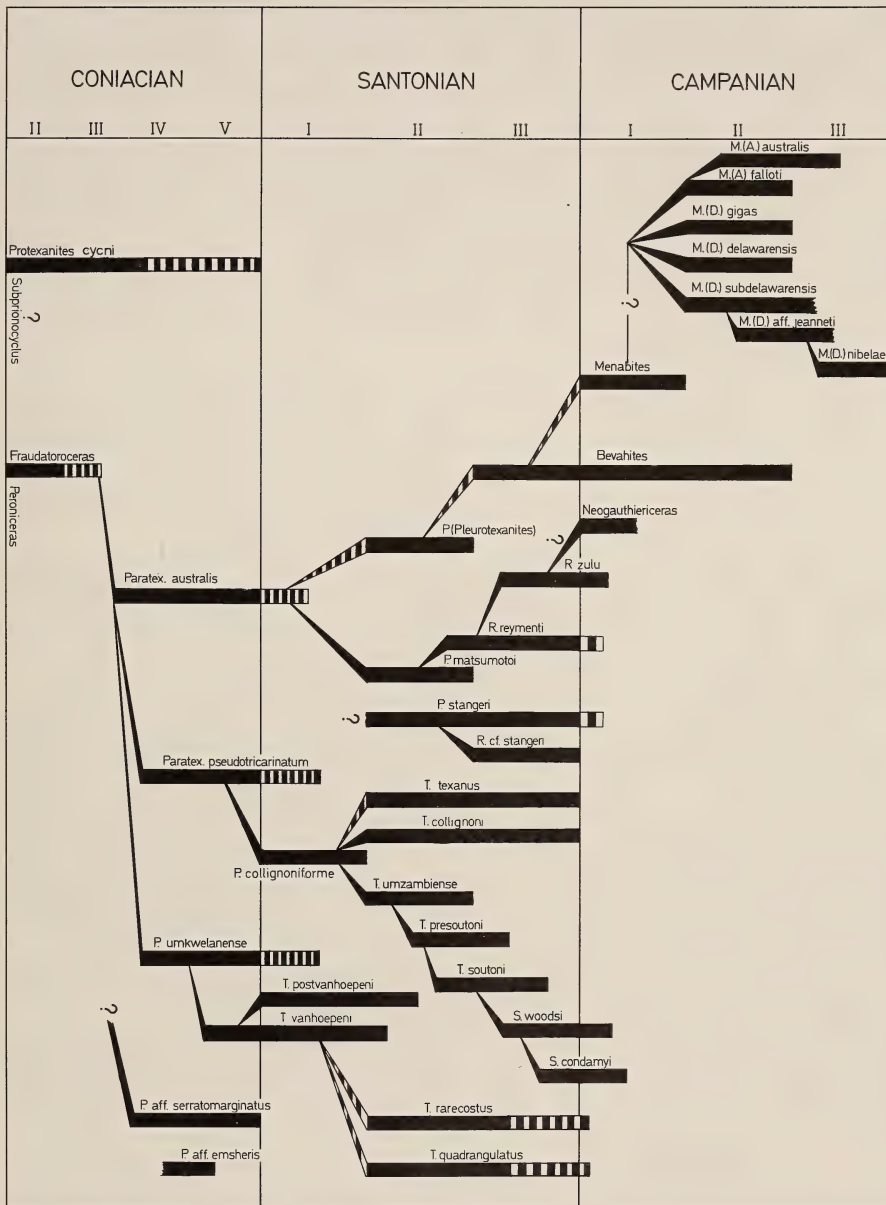


Fig. 266. Suggested lines of evolution within Texanitinae as inferred from South African material.



to derive *Bevahites* from *Pleurotexanites*, which in turn may give rise to *Menabites* s.l. This is basically the same view held initially by Matsumoto (1955: 43, table 1), but lately he (Matsumoto 1970: 299) and Young (1963: 107) favour the alternative of deriving *Menabites* (*Australiella*) from *Protexanites*. Matsumoto (1970: 299) also dismisses *Pleurotexanites* as an ancestor of *M.* (*Australiella*), and considers these two taxa to be sibling offshoots of *Protexanites* s.s.

This view seems to be based on the alleged occurrence of two species of *Australiella*, *A. austinensis* and *A.* sp. aff. *pattoni*, in strata of Santonian age. Both these species lack precise stratigraphic data, and the authors prefer deriving *Australiella*, *Delawareella*, and possibly *Bererella* via *Menabites* s.s. from *Bevahites*, a view supported by the stratigraphic occurrence of these taxa in Madagascar and Zululand.

*Plesiotexanites* may be regarded as a *Paratexanites* with a variably developing lateral tubercle. Through fusing of the external (5) tubercles in *Plesiotexanites*, the tricarinate venter of *Reginaites* may be derived. Development in *Reginaites* tends towards discarding of the lateral (2) *Plesiotexanites* tubercle, and possibly also a sharpening of the venter and gradual weakening of the lateral keels, possibly resulting in *Neogauthiericeras*.

*Plesiotexanites* also probably gives rise to part of *Texanites*, e.g. *T. collignoni*, and possibly *T. umzambiense* and *T. texanus*. *Submortonicerases* is derived from *Texanites* through reduction of the umbilical diameter in the South African material, and supports Young's (1963: 90) views concerning the relationship between *Texanites shiloensis* and *Submortonicerases tequesquitense*.

Part of *Texanites* appears to be derived directly from *Paratexanites* without passing through a *Plesiotexanites* stage, e.g. *T. vanhoepeni* and *T. postvanhoepeni*.

One distinct evolutionary trend noticeable in the South African texanitids is the tendency towards reduction of umbilical width and ornament in younger forms. A striking example of this is the sequence starting with *T. umzambiense*, through *T. presoutoni* and *T. soutoni* to *Submortonicerases woodsi* and *S. condamyi* (Fig. 131). Another possible sequence is that of *M.* (*Delawareella*) *subdelawarensis* through *M.* (*D.*) sp. aff. *jeanneti* to *M.* (*D.*) *nibelae*.

In addition, there appears to be a reduction of overall size in these two lineages, but here the trend is not very distinct.

Through reduction of the umbilical width and ornament, and also overall size and length of the body chamber, the shell becomes more streamlined and consequently hydrodynamically stable. This seems to indicate a more active mode of life, and, possibly, a deeper water habitat.

#### PALAEOBIOGEOGRAPHY

The palaeobiogeographic distribution of the Texanitinae during the Late Coniacian to Early Santonian, Santonian s.l., and Early to Mid-Campanian, as shown in Figures 267–269, is basically the same as that shown by Collignon (1948: 52).



Fig. 267. Palaeobiogeography of Texanitinae during Coniacian to Early Santonian time (Map after Smith *et al.* 1973, fig. 7.)

The geographic, as well as the biological origin (see p. 348) of the Texanitinae is obscure, and detailed stratigraphic collection is necessary to substantiate Collignon's assumption that radiation started in western Europe. Current data show that *Protexanites* and *Paratexanites* species already occur in western and central Europe, North Africa, the Gulf Coast region of North America, Hokkaido, and Zululand by Late Coniacian time. Wiedmann (1960), however, reports *Protexanites bourgeoisi*, *Protexanites* cf. *bontanti*, and *Protexanites* sp. nov. from the Lower Coniacian of the Vascogotic region of the Iberian Peninsula, which may substantiate Collignon's views. The rate of dispersion thus seems to have been very rapid.

During Santonian time, four main regions of development were already established: western and central Europe and the Middle East; the Gulf Coast and adjacent areas of North America; Hokkaido and environs; and Madagascar and South Africa; with minor centres in north Africa (Algeria), west Africa (Nigeria and Cameroons), south-western Africa (Angola), and northern South America (Venezuela and Peru). In terms of numbers and diversity, the centre of maximum development appears to be Madagascar and South Africa.



Fig. 268. Palaeobiogeography of Texanitinae during Middle to Late Santonian time.  
(Map after Smith *et al.*, 1973, fig. 7.)

Even though the majority of species in Santonian time *appear* to be endemic to these four main regions, faunal exchange did take place on a limited scale, as shown by the distribution of *Plesiotexanites stangeri* (Madagascar, South Africa, Hokkaido, and Gulf Coast).

During Early and Middle Campanian times, endemism and development of the Texanitinae seems to have reached its peak. Again Madagascar and South Africa seem to have been the centre of development as exemplified by the large number of *Menabites* s.l. and *Submortonicerases* species, even if excessive taxonomic splitting is taken into account. In Europe, texanidine species decreased numerically, and this region was now of subordinate importance to North America and Hokkaido. Faunal interchange now was even more limited than during Santonian time, and restricted to a few species, e.g. *M. (Delawarella) delawarensis* (Zululand and North America), *M. (Delawarella) campaniensis* (North America and Europe), *Submortonicerases chicoense* (North America and Subantarctic Islands).

The demise of texanitids towards the end of Middle Campanian time appears to have been virtually instantaneous, following a period of virtual maximum development and occasional gigantism in Zululand, and no texanitids are known from the Upper Campanian sediments.





Fig. 269. Palaeobiogeography of Texanitinae during Early to Middle Campanian time. (Map after Smith *et al.*, 1973, fig. 7.)

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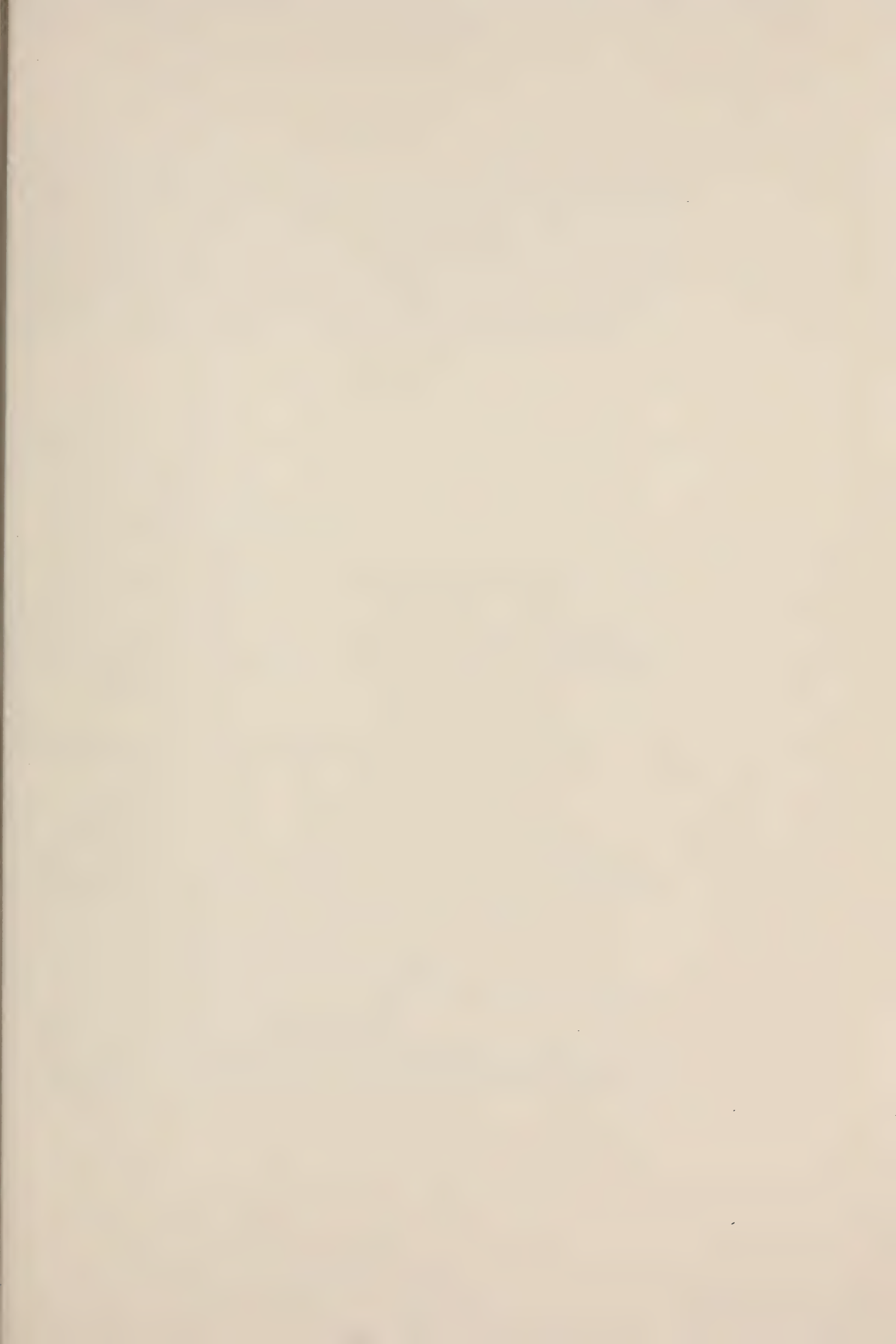


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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierii* Philippi, 1861: 87.

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

*Holotype*

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

*Capital initial letters*

- (a) The Figures, Maps and Tables of the paper when referred to in the text  
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names  
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives  
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

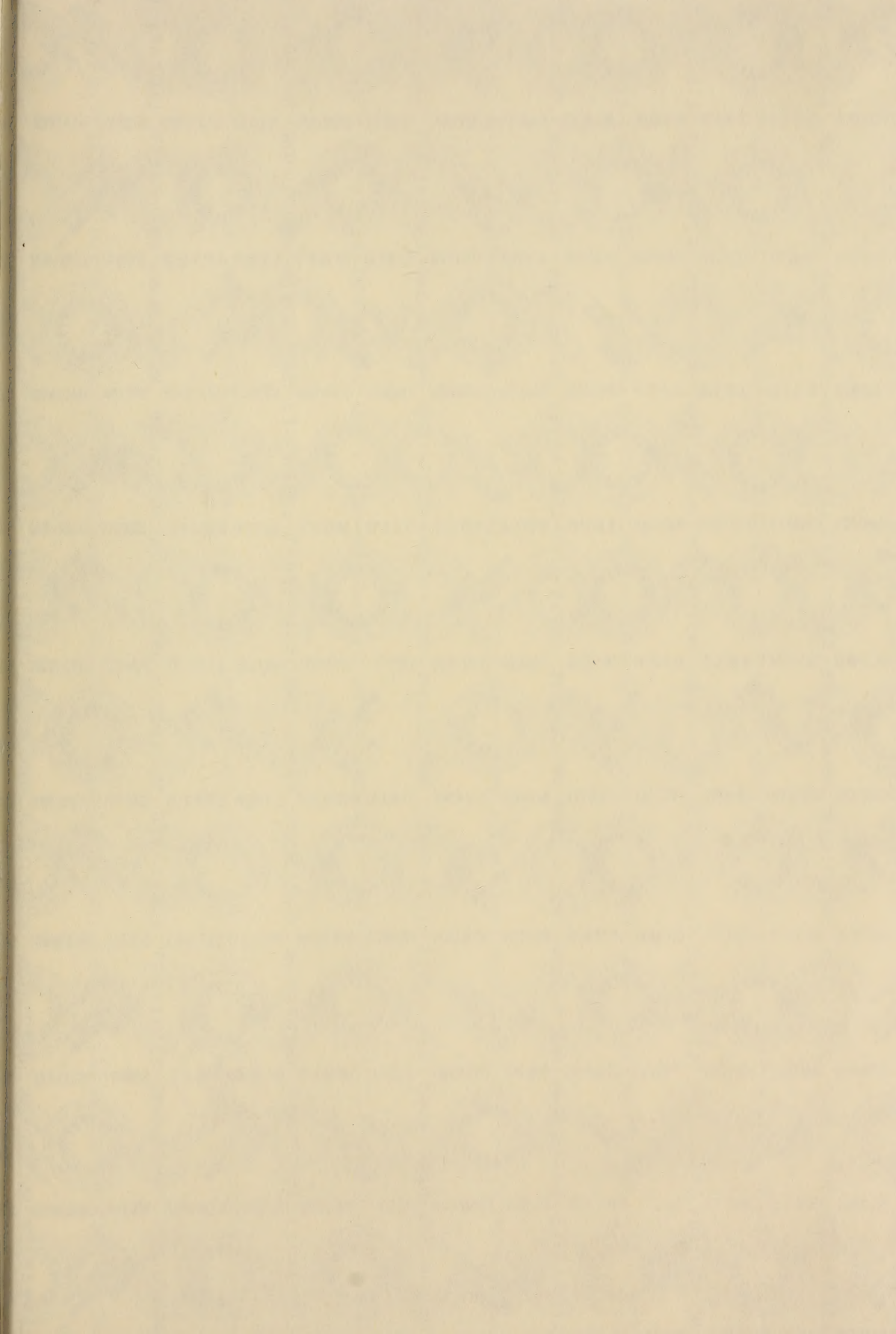


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CRETACEOUS FAUNAS FROM ZULULAND  
AND NATAL, SOUTH AFRICA  
THE AMMONITE SUBFAMILY TEXANITINAE  
COLLIGNON, 1948













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